EVOLUTIONARY AND BIOGEOGRAPHIC PATTERNS OF TRILOBITES DURING THE END ORDOVICIAN MASS EXTINCTION EVENT

BY

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Abstract: The end Ordovician mass extinction event is believed to have been caused by a geologically brief, sudden onset glacial period that interrupted a period of extreme greenhouse conditions. The cause of this icehouse is a matter of contention, but recent a recent work proposes that a nearby gamma-ray burst could have affected the Earth's atmospheric chemistry and pushed the climate from a greenhouse into an unstable icehouse. Survivorship patterns of trilobites and their larval forms appear to agree with this theory. In order to further explore the Ordovician extinction, I conducted three individual paleontological studies to test macroevolutionary and biogeographic patterns of trilobites across the extinction. The first study is a phylogenic and biogeographic analysis of the family Homalonotidae Chapman 1890, the second is a similar analysis of the subfamily Deiphoninae Reed 1913, and the third is a GIS study of species ranges of the subfamily Deiphoninae.

The End Ordovician; an ice age in the middle of a greenhouse

Introduction

With millions of years of Earth history to study, it is interesting that so much attention is devoted to the rare and relatively short lived time intervals that represent Earth's major mass extinctions. Perhaps this interest is twofold. On the one hand, there is a fair degree of self-interest in studying extinction considering the present biodiversity crisis we now face. On the other hand, these periods of time have had an incredible effect on life's history. These cataclysmic times represent periods of environmental and ecological abnormality amidst millions of years of relative stability. As such, these mass extinctions are times of incredible change, which can be studied both evolutionarily as well as ecologically. When viewed through an evolutionary framework, mass extinction events represent unique time periods in the history of life. These ecological crises prune the tree of life, removing families and killing off entire lineages, perhaps effectively at random (Raup 1981). Those lineages lucky enough to survive the catastrophe continue and diversify. Often, it is by this seemingly random removal of organisms that large scale evolutionary changes can take place. Consider the present state of our world. The dominant large terrestrial vertebrates might be considered the mammals. However, had the non-avian dinosaurs not met with an untimely demise at the end of the Cretaceous, mammals would probably never have been able to diversify into the numerous forms that we see today. It is for this reason that the study of mass extinction events is incredibly important to evolutionary biology. Mass extinctions are essentially historical "turning points" that affect the evolution of all of the Earth's biota on a grand scale.

Mass extinctions can also be studied as ecological experiments. Ultimately, mass extinctions represent times of ecological upheaval in which climate may shift and ecological

niche space can be destroyed. By studying both the causes of these ecological perturbations, as well as the affect that these changes have on the biota, we are able to better understand how life reacts under times of ecological stress. This in turn can help us predict the patterns that we might expect in future mass extinctions. This type of study is of particular importance in our present biodiversity crisis.

The end Ordovician mass extinction is a unique time period that offers a great deal of study material to geologists interested in both the ecological and evolutionary aspects of mass extinctions. The end Ordovician mass extinction is a time of great ecological upheaval. The cause of this massive die off has long been considered to be a glacial period (Berry and Boucot 1973, Sheehan 1973). Although aspects of this interpretation appear to be sound, there is still a great deal of debate about the timing of the glacial event as well as its forcing mechanism. The original interpretation proposed by Berry and Boucot (1973) was that the glacial period might have lasted millions of years and that global cooling was gradual. Recent evidence (Melott et al 2005, Brenchley et al. 1994) suggests that the glaciation was incredibly sudden and brief, possibly lasting only a few hundred thousand years. Furthermore, it appears that this glacial period occurred in the middle of a greenhouse climate. The extinction patterns in the end Ordovician glacial period are also intriguing, especially the patterns found in trilobites. Trilobite species with cosmopolitan biogeographic ranges preferentially go extinct while more endemic species are more prone to survive (Chatterton and Speyer 1989). This is contrary to the pattern frequently identified by Stanely (1979), Vrba (1980), Eldridge (1979) and others, who argued that organisms with larger biogeographic ranges tend to have lower extinction rates than those with smaller, more endemic ranges. Yet, in the Ordovician extinction it is the endemic species that tend to survive.

This paper will focus on previous research that has been conducted on the Ordovician mass extinction. Furthermore, several of the major unresolved issues concerning the causes of the glaciation as well as the patterns of the extinction will be emphasized; this paper will conclude with a discussion of new research that hints at a possible forcing mechanism for the sudden onset of glaciation.

Early Research: The Discovery of the Glacial Period

Some of the first scientists to invoke a massive glacial period at the end of the Ordovician were Berry and Boucot (1973). Berry and Boucot were interested in explaining a global pattern within the sedimentary record. During the early Silurian there was substantial evidence of onlap deposits. Prior to this rapid rise of sea level, there is some evidence (Kielan 1959) that the sea level had been steadily dropping during the late Ordovician. What could have caused this global fall and rise of sea level? One explanation could have been tectonic processes, such as orogenic events. These processes could raise and lower the land, thus changing the land's position relative to sea level. However, in order for this mechanism to result in a seemingly global sea level rise, there would need to be synchronicity amongst all tectonic events occurring on the planet. Berry and Boucot (1973) did not find any significant time correlation across regions between the tectonic events that occurred during the end Ordovician. Thus, another mechanism needed to be invoked in order to explain this global phenomenon.

Again, the clues to discovering this mechanism came from studying the sedimentological record. During the late Ordovician, gravel and cobble deposits were found in North Africa, which were interpreted as being glacially derived sediments (Beuf et al 1971;

Destombes 1968; Dow et al. 1971). Furthermore, late Ordovician age sedimentary deposits were found in Europe that were interpreted as being ice rafted debris (Arbey and Tamain 1971; Dangeard and Dore 1971; Shönlaub 1971). These sedimentary deposits suggested that there might have been an increase in glacial ice during the late Ordovician. Since the presence of this ice correlated with the estimated time of sea level fall, Berry and Boucot (1973) proposed that massive glaciation was the mechanism responsible for the drop in sea level. The concept behind this theory is similar to a phenomenon which occurred during the recent Pleistocene glaciations: Newell and Bloom (1970) observed that during the last glacial period the sea level was approximately 100 meters lower than it is at present. This is because ice that rests on land effectively traps water and prevents it from reaching the ocean. As more land locked ice builds up, it traps more water from reaching the oceans and the sea level falls. This is the mechanism that Berry and Boucot invoked to explain the sedimentological pattern observed at the end Ordovician. During the late Ordovician, the onset of a glacial period resulted in the lowering of global sea level as water was trapped in continental glaciers. As the glaciers melted, the water was returned to the oceans and sea level rose. This explained the onlap deposits found in the early Silurian. Berry and Boucot (1973) concluded that this process was probably very gradual, and that the end Ordovician glacial period lasted millions of years, unlike the recent Pleistocene glaciations.

This glacial process was supported by Sheehan (1973) who cited a biogeographic pattern of brachiopod evolution that he deemed consistent with glacially driven eustatic changes. Prior to the end Ordovician, there existed two major brachiopod provinces, a North American province and an Old World Province. After the extinction event, the North American province was gone and was replaced by species that were derived from the Old World faunas. Sheehan (1973) believed that this faunal interchange, as well as the extinction of the North

American fauna, was caused by eustatic sea level changes during the glacial event. Prior to the glaciation, shallow epicontinental seas (approximately 70 meters deep) covered much of North America (Foerste 1924). These epicontinental seaways represented the habitat for the North American brachiopod fauna. During the 100 meter sea level drop proposed by Berry and Boucot (1973), these epicontinental seaways would have almost entirely dried up. Such a massive reduction in habitat space would have greatly stressed the North American brachiopods, ultimately resulting in their extinction. This habitat space would then have been repopulated by the nearby Old World fauna, which would have been less affected by the extinction because the higher European topography meant that the Old World brachiopods were adapted to shelf niche space and not epicontinental seaways (Sheehan 1975). Sheehan envisioned this process as being gradual, with the North American faunas going extinct over the course of the glacial period and the Old World faunas steadily replacing and out competing the local fauna (1973, 1975). However, he admitted that biostratigraphy of the Late Ordovician period was poor and thus any time correlation must be taken with a grain of salt.

Fast or Slow: The Changing Face of the Ordovician Glaciation

During the next twenty years, there was a great deal of research concerning the timing of the glacial onset as well as how long the glacial period lasted. Originally, the glaciation was thought to have started in the Caradoc and continued into the Silurian. However, this estimated glacial duration met with a fair degree of contention. The Caradoc had originally been established as the onset of glaciation because of faunal assemblages found in glacial sequences in the Sahara (Hambrey 1985). However, these assemblages had been described as being older preglacial clasts that had been ripped from the bedrock and incorporated into the glacial

sediments (Spjeldnases 1981); thus they could not be used to date the sequence. Crowell (1978) had suggested that the glacial period extended far into the Silurian. This conclusion was based on tillite deposits found in South America that were believed to be Wenlock in age (Crowell 1978). However, Boucot (1988) called this age constraint into question, citing that the paleontological record in the area was insufficient for use in biochronology. Furthermore, he suggested that the tillites were probably from the Ashgill.

An Ashigillian date for the glacial episode was further corroborated by two other pieces of evidence. First, Brenchley et al (1991) identified Ashgillian age glacial-marine diamictites that were interbedded with fossiliferous deposits. Second, Brenchley et al (1994) conducted a global geochemical study analyzing $\delta^{18}O$ and $\delta^{13}C$ of brachiopod shells found in the midwestern United States, Canada, Sweden, and the Baltic states. They were unable to consistently use brachiopods of the same genera and instead used a wide variety of species but found that their data clustered together relatively well. This helped to ensure that any pattern they found in their data was an actual signal and not just error caused by varying biotic isotopic fractionation. The results of this study showed that there was a sharp positive increase in $\delta^{18}O$ during the Ashgill. $\delta^{18}O$ concentrations returned to their pre-Ashgillian state at the end of the Ordovician. This increase in $\delta^{18}O$ concentration is consistent with what would be expected from a glacial event. Global cooling and accumulation of negative $\delta^{18}O$ ice would cause global ocean water to become enriched in ^{18}O, resulting in the positive shift in $\delta^{18}O$. Once the ice melted and the temperatures returned to normal, the $\delta^{18}O$ concentration returned back to its pre-Ashgillian state. This geochemical evidence indicates that the onset of glaciation occurred during the Ashgill and that the glacial period was incredibly brief. But what could have caused this glaciation?

The results of Brenchley et al (1994) become even more peculiar when you take into account paleoclimatic studies of the Ordovician and Silurian. Research indicates that the atmospheres of the late Ordovician and early Silurian had very high concentrations of CO_2 (Berner 1990, 1992; Crowley and Baum 1991). High concentrations of CO_2 would act to keep the climate of the late Ordovician in a greenhouse condition. How could a glacial period exist in the middle of a greenhouse? Brenchley et al (1994) proposed one possible mechanism that was consistent with their $\delta^{13}C$ data. When the $\delta^{18}O$ data shifts towards the positive, there is a contemporaneous shift in the $\delta^{13}C$ towards the positive as well. This shift in $\delta^{13}C$ was envisioned as an increase in marine productivity because of increased cool deepwater production. Before the onset of glaciation, the deepwater of the Ordovician would have been warm and poorly circulated (Railsback et al. 1990). If global temperatures cooled, the ocean water would have cooled as well which would help to increase oceanic circulation. This would have made the oceans rich in nutrients and increased the productivity of the oceans, which in turn would act to remove CO_2 from the atmosphere, effectively lowering the Earth's temperature and allowing for the brief icehouse conditions to occur (Brenchley et al 1994). Although this theory helps to explain why a glacial period could persist in the midst of greenhouse conditions, it still requires that some initial forcing mechanism act to cool the Earth's temperature. The forcing mechanism that was cited by Brenchley et al. (1994) was the migration of Gondwana. As the continent migrated pole-ward, it would have accumulated ice and snow, thus increasing the Earth's albedo and decreasing global temperature (Crowley and Baum 1991). However, there is a problem associated with this mechanism. The migration of Gondwana is a tectonic forcing mechanism, and tectonism usually operates on million year time scales. Even if the onset of glaciation was somehow sudden (if the Earth needed a threshold albedo value to spontaneously glaciate), it would still take millions of years until the

glacial period ended. This does not coincide with the brief glacial period proposed by Brenchley et al (1994). Thus, it seems counterintuitive for the migration of Gondwana to be the initial forcing mechanism for the glaciation.

A recent study by Melott et al (2004) proposes that the Ordovician glaciation could have been caused by a gamma ray burst (GRB). Such an event could result in a sudden and brief glacial period on the order of time that is predicted by Brenchley et al (1994). The theory is as follows: A GRB from a star roughly 5,000 light years away sends high-energy waves in the form of photons out into space (physical modeling has shown that GRB's at this distance from Earth have likely occurred at least once in the last 1Ga). These high-energy waves make it to Earth and begin initiating various atmospheric reactions. The net effect of these reactions is twofold. First, the increased cosmic radiation would destroy ozone, thus thinning the planet's ozone layer. Second, there would be increased production of NO_x gases. These opaque gases would build up in the atmosphere, darkening the Earth's skies and preventing sunlight from reaching its surface. This build up of NO_x gases would result in global cooling. Melott et al (2004) estimated that the GRB would have lasted only a matter of seconds, but the effects that it would have had on the atmosphere would have taken years to equilibrate (Laird et al 1997). This theory is very interesting because it offers a mechanism by which the Ordovician glaciation could have occurred suddenly during greenhouse conditions. Furthermore, it explains why the glacial period was so brief. After the GRB event was over, the NO_x gases in the atmosphere responsible for global cooling began to slowly decay over the course of several years. However, the effects of this initial cooling caused by the GRB probably contributed to other factors which helped to prolong global cooling, such as increased albedo due to ice accumulation, or the increased ocean productivity due to increased circulation as proposed by Brenchley et al (1994). This ultimately would have resulted in the brief and unstable icehouse

conditions at the end Ordovician. The GRB hypothesis might also explain some of the extinction patterns during the Ordovician extinction, in particular those pertaining to trilobites.

A final issue with glaciation as the sole cause of the end Ordovician mass extinction is that we know that other times of profound glaciation in Earth history are not associated with mass extinctions. For instance, relatively few extinctions have occurred on Earth in the last few million years (excluding the impact of our own species) during a time of relatively extensive glaciation.

Trilobite Extinction and Larval Form

Chatterton and Speyer (1989) drew attention to an unexpected pattern associated with the late Ordovician extinction. They studied trilobite extinction patterns and related survivability to the proposed lifestyle and larval forms of each family. What they discovered was that the greater the duration of an inferred planktonic larval phase, the greater the probability of extinction. Trilobites that were inferred to have planktonic larval stages and benthic adult stages were more likely to go extinct than trilobites that spent their entire lives in a benthic stage. Furthermore, trilobites that were most affected by the extinction (and subsequently entirely wiped out) were those organisms that had an inferred pelagic adult stage. Aspects of this pattern may be the opposite of what we might tend to expect: Species with planktonic larval stages or pelagic adult stages would tend to have larger biogeographic ranges than species that are purely benthic. As such, these planktonic or pelagic trilobites would have tended towards being more ecologically generalized, whereas the benthic species would have tended to be more specialized and endemic. Organisms that are ecological generalists and have broad geographic ranges usually have very low extinction rates, whereas narrowly distributed

specialists tend to have very high extinction rates (Vrba 1980). Therefore, it would be natural to assume that generalists would be better buffered against extinction than specialists. However, in the end Ordovician it is the more narrowly distributed putative specialist organisms that are best suited to survival, while the more broadly distributed putative generalists are more at risk. Chatterton and Speyer (1989) explained this pattern as being the result of a trophic cascade resulting from the effects of global cooling. In particular, they argued that as the ocean temperatures cooled during the glacial event, the lower water temperatures would have eventually acted to reduce the productivity of phytoplankton (Kitchell 1986, Kitchell et al. 1986, Sheehan and Hansen 1986). Since the plankton was the basis for the food chain, there would have been increased extinction up the trophic levels in planktonic and pelagic organisms. Benthic trilobites would have been buffered from the effects of this trophic cascade scenario because they were probably detritus feeders who would have eaten the remains of the dead pelagic and planktonic organisms.

Although this is one possible scenario that could have resulted in this extinction pattern, another explanation emerges if we view the extinction as being caused by a GRB as proposed by Melott et al (2004). One of the proposed effects of a GRB is thinning of the ozone layer. If the ozone layer thinned during the end Ordovician, this would have allowed a larger flux of high-energy ultraviolet (UV) radiation to reach the surface of the planet, increasing rates of deadly mutations. Organisms that lived at the surface of the oceans or high up within the water column would have been more affected by this increase in UV radiation than benthic organisms that would have been better shielded by surrounding sediments. Therefore, the planktonic larval forms and pelagic trilobites would have already been under much more stress than their benthic counterparts at the onset of glaciation, possibly even before major global cooling had set in. The increase of high-energy UV radiation reaching the Earth's surface,

coupled with the sudden glacio-eustatic changes and global cooling would have hit the Earth's biota in a devastating one-two punch.

I propose a third process that might also help to explain the trilobite extinction pattern observed at the end Ordovician. Vrba (1993, 1995) has shown that fluctuations in paleoclimate could result in speciation. According to Vrba (1993, 1995) as climates change, the organisms that live within their respective climatic ranges will track their preferred climate. In times of extreme climate change, such as the onset of an icehouse condition, the species ranges of tropical and temperate species would begin to shrink and move towards the equator. As the species ranges shrink, there is a greater probability that small populations could become reproductively isolated from the main population. If this situation persists for long enough, these small populations will speciate by means of allopatric speciation. Thus, somewhat paradoxically, the habitat destruction caused by massive global change could also act to temporarily increase levels of speciation. Applying this theory to the end Ordovician, we would expect that as global cooling shrunk the biogeographic ranges of trilobites, they too would experience an increase in speciation rate that might have helped them to stave off the heightened extinction rates. In endemic species such as the trilobites with benthic larval stages, perhaps it would have been easier for smaller populations to become reproductively isolated by habitat destruction due to the specificity of their environmental constraints. On the other hand, generalist species might have been more difficult to reproductively isolate long enough to result in speciation. The net result would be that generalist trilobites would have been given less of a boost to their speciation rate during the glacial episode than endemic species and would therefore have been less buffered against the effects of the raised extinction rates. A detailed study of extinction and speciation rates of planktonic larval and non-planktonic larval trilobites over the course of the Ordovician would be necessary in order to test this hypothesis.

Introduction to the Thesis

The following thesis consists of three individual paleontological studies aimed at gaining a deeper understanding of macroevolutionary patterns and processes during the end Ordovician mass extinction event. In particular, each study explores the biogeographic and evolutionary patterns of trilobites across the event. The first study is an evolutionary analysis of the trilobite family Homalonotidae Chapman 1890 in which a phylogenetic hypothesis of relatedness was generated for the group and then used to conduct a biogeographic analysis. The second study is an evolutionary analysis of the cheirurid subfamily Deiphoninae Reed 1913 in which a second phylogenetic hypothesis of relatedness was generated and used to conduct a biogeographic analysis. The final study uses GIS and PaleoGIS to estimate species ranges for members of the Deiphoninae occurring during the Ordovician and Silurian.

Phylogenetic and Biogeographic Analysis of Ordovician Homalonotid Trilobites

Introduction

The Homalonotidae Chapman 1890 is a distinctive group of relatively large Ordovician-Devonian trilobites. They are not especially diverse, although they are common in nearshore environments. However, because of their shovel-like cephalon and tendency towards effacement, they have received some interest among paleontologists in general and trilobite workers in particular. There have been debates about taxonomy of the Homalonotidae. These are caused in part by the group's close evolutionary affinity to its sister taxon, Calymenidae Burmeister 1843 (see Edgecombe *in* Novacek and Wheeler 1992 for a phylogeny of trilobite families to support this relationship). In particular, this has caused paleontologists to suggest different family-level assignments for some genera (see Whittard 1960, Vanek 1965, Whittington 1966, Thomas 1977, Henry 1980, Henry 1996 for varying opinions on homalonotid classification). Also, the Ordovician homalonotids are rather distinct, such that there is a morphological discontinuity between these and the more derived Silurian and Devonian forms (Thomas 1977). Here I revisit the issue of homalonotid taxonomy using a phylogenetic analysis. My focus is primarily on Ordovician homalonotids since these are most critical from the perspective of reconstructing taxonomic patterns in the group because they are phylogenetically basal, and also this study may provide information on the number of taxa affected by the end Ordovician mass extinction. On the whole, the reconstructed phylogenetic patterns correspond most closely to Thomas' (1977) taxonomy of the family. Further, I use the phylogenetic hypothesis to reconstruct biogeographic patterns in the group by conducting a modified Brooks Parsimony Analysis (see Lieberman and Eldgredge 1996; Lieberman 2000).

The biogeographic analysis makes it possible to consider the role of biogeography in the end Ordovician mass extinction.

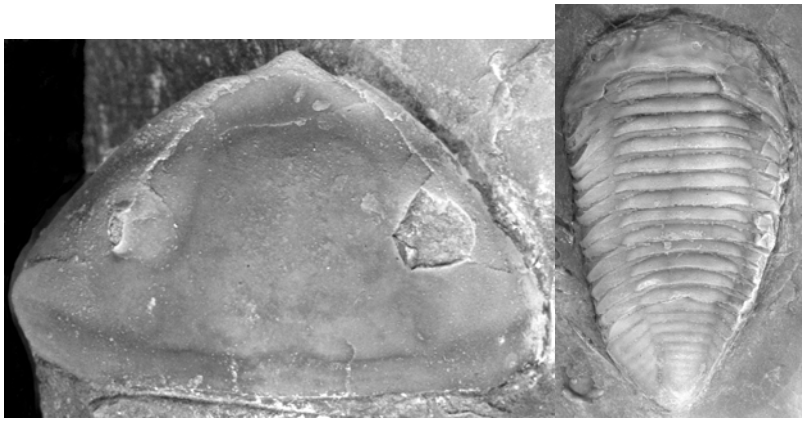

Fig 1: *Trimerus delphinocephalus* cephalon (left) YPM 204412 and thorax and pygidium (right) YPM 204408. Middle Silurian, Clinton Group, Rochester Shale. Collected in Lockport, New York.

Materials Analyzed

Specimens from the Yale Peabody Museum (YPM) YPM 7449A, 7449B, 33872, 33870, 204407, 204410, 6575, 204408, 204412, and 204411 and Harvard's Museum of Comparative Zoology (MCZ) MCZ 190759, 190778, 190828, and 190832 were used in the analysis. For key references on homalonotids, see Whittard (1960), Whittington (1965), Thomas (1977), Henry (1980), Whittington (1992), Whiteley et al (2002), Hammann (1983), Dean (1961), and Dean & Martin (1978).

Methods

Morphological terminology follows Whittington et al. (1997).

Taxa Analyzed- Sixteen taxa were considered in this phylogenetic analysis**.** *Neseuretus* Hicks, 1873 was used as the outgroup; it is widely considered to be a basal calymenid. For instance,

see Whittard 1959, Thomas 1977, and Henry 1980; though see Sdzuy in Moore 1959 and Hupé 1953 for a contrary viewpoint. The taxa analyzed in the ingroup had been originally assigned to *Plaesiacomia* Hawle and Corda, 1847, *Trimerus* Green, 1832, *Platycoryphe* Foerste, 1919, *Calymenella* Bergeron, 1890, *Brongniartella* Reed, 1918, *Eohomalonotus* Reed, 1918, and *Colpocoryphe* Novák in Perer, 1918. The hierarchical placement of several of these genera has been a matter of contention. Although traditionally placed with Homalonotidae, Henry (1980) had argued that *Colpocoryphe* belonged in Calymenidae based on hypostomal structures that suggested the genus was closely related to *Neseuretus*. He also argued that *Platycoryphe* and *Calymenella* should be removed from Homalonotidae and placed in Calymenidae, primarily based on thoracic characters (Henry 1996). However, I include these three genera in Homalonotidae based on characters of the cephalon, glabella, and pygidium that I discuss more fully below.

Character Analysis- The characters used for this phylogenetic analysis come from the dorsal side of the mineralized exoskeleton. Hypostomal characters were not included because the hypostome is rarely preserved in homalonotids and for too many of the taxa analyzed incomplete information was available. The characters are listed below in approximate order from anterior to posterior position on the organism.

1. anterior margin outline --- dorsal view (convex = 0 / not convex = 1)
2. preglabellar field expansion (sag.) --- dorsal view (roughly twice length of LO [sag.] = 0 / roughly the length of L0 [sag.] = 1)
3. cephalic outline --- dorsal view (lanceolate = 0 [anterior margin width > width of L0 and lateral margin weakly convex] / subovate = 1 [anterior margin width < width of L0

and lateral margin strongly convex] / triangular = 2 [anterior margin width ≤ width of L0 and lateral margin weakly convex])

4. glabellar furrows (encroaching sagittal axis of glabella = 0 / restricted to lateral margins or indistinct = 1)
5. anterior margin of glabella --- dorsal view (not strongly convex = 0 / strongly convex = 1)
6. inflation of anterior margin of cephalon --- dorsolateral view (inflated = 0 / not inflated = 1)
7. ala distinctness --- dorsal view (distinct = 0 / indistinct or absent = 1). The ala is a semicircular lobe adjacent to the basal glabella outlined by a furrow of variable depth.
8. glabella convex on entire lateral margin --- dorsal view (present = 0 / absent = 1)
9. glabella expands laterally in the medial section of L1 to form a bell shape --- dorsal view (absent=0/present=1)
10. glabella posterior margin --- dorsal view (strongly convex = 0/ not strongly convex = 1)
11. shape of posterior part of fixigenae --- dorsal view (subangular = 0 / rounded = 1)
12. posterior fixigenal angle --- dorsal view, relative to transverse line (30-40º = 0 / >55º = 1)
13. lateral processes on axial rings (present = 0 / absent = 1)
14. cephalon lateral convexity --- lateral view (distinct = 0 / indistinct = 1)
15. occipital ring (thickest medially, with anteriorly directed lateral wing-like processes = 0 / uniform thickness, posteriorly curved, with indistinct or absent lateral wing-like processes = 1 / uniform thickness or widest medially, but parallel to thoracic axis, with anteriorly directed lateral wing-like processes indistinct or absent = 2) *the specimen

used to code *Plaesiacomia exul* did not possess a complete occipital ring so the coding for this taxa was accomplished by extrapolation, using what was left of the structure.

16. glabellar furrows --- dorsal view (deep = 0 / shallow or absent = 1)
17. pygidial axis shape --- dorsal view (funnel-shaped = 0 / ovate = 1)
18. swollen tubercle on pygidial axial terminus --- dorsal view (present = 0 / absent = 1)
19. posterior pygidial pleurae (distinct = 0 / indistinct = 1)
20. pygidial outline --- dorsal view (conical = 0 / subconical = 1)
21. number of pygidial axial furrows ($\geq 5 = 0$ / $\leq 3 = 1$)
22. posterior pygidial margin --- dorsal view (convex = 0 / concave = 1)
23. a coaptive pygidial groove, parallel to lateral pygidial margins that connects to anterior cephalic margin during enrollment --- dorsal view (absent = 0 / present = 1)
24. pygidial lateral convexity --- dorsal view (distinct = 0 / indistinct = 1)
25. pygidial dorsal convexity --- lateral view (pronounced = 0 / not pronounced = 1)
26. lateral expansion of the last axial segment of the pygidial axis --- lateral view (absent = 0 / present = 1)

Phylogenetic Analysis- The data were analyzed using PAUP 4.0 (Swofford 1998). A branch and bound search was used to determine the most parsimonious tree for this data matrix. All multistate characters were treated as unordered. Bootstrap and Jackknife statistical tests, as well as a test of Bremer (1988) support, were performed to assess the statistical strength of my results. The Bootstrap and Jackknife tests were performed using PAUP (Swofford 1998) and were analyzed heuristically with 1,000 replicates; five most parsimonious trees were sampled at each replication. A Bayesian analysis using MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2005) was also performed on the data, with the nst=6 and rates=invgamma. This allows rates

of change to vary between and within transformation series. The mcmc went through 10,000,000 generations, sampling every 1000 generations. All matrix data were compiled into Nexus files using Macclade v.4.08 (Maddison and Maddison 2005) and Mesquite v.2.01 (Maddison and Maddison 2007) and trees were generated using FigTree v.1.1.2 (Rambaut 2008).

Specific Taxa Analyzed- Plaesiacomia exul (Whittington 1953), *P. vacuvertis* Thomas 1977, *P. oehlerti* (Kerforne 1900), *Colpocoryphe arago* (Rouault 1849), *C. roualti* Henry 1970, *Calymenella boisselli* Bergeron 1890, *C. alcantarae* Hammann & Henry 1978, *Brongniartella bisulcata* (M'Coy 1851, ex Salter, MS.), *B. trentonensis* (Simspon 1890) (YPM 7449A and 7449B, MCZ 190828 and 190832), *Trimerus delphinocephalus* (Green 1832) (YPM 33872, 33870, 204407, 204410, 6575, 204408, 204412, and 204411), *Eohomalonotus sdzuyi* Hammann & Henry 1978, *Platycoryphe dyaulax* Thomas 1977, *P. dentata* Dean 1961, *P. christyi* (Hall 1860), and *P. vulcani* (Murchison 1839) for a total of fifteen ingroup taxa. *Neseuretus vaningeni* Dean & Martin 1978, was chosen as the outgroup for the analysis because it is a well-preserved, complete specimen of *Neseuretus* from the lower Ordovician of eastern Newfoundland.

Table 1: Homalonotid character matrix

Taxon/characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Neseuretus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
delphinocephalus	0	0	2	1	0	1	1	1	0	1	1	1	1	1	2	1	0	1	0	0	0	0	0	1	1	0
dyaulax	1	1	2	1	0	1	0	1	0	1	1	1	1	1	2	1	0	1	0	1	0	0	0	1	1	0
exul	1	1	1	1	0	1	1	0	0	1	1	0	1	1	1	1	0	1	1	0	?	1	?	?	?	0
dentata	0	1	2	0	0	1	0	0	0	1	1	1	1	1	2	1	0	0	0	1	0	0	0	1	0	0
christyi	1	1	2	0	0	1	0	0	0	0	1	1	1	1	2	1	0	1	0	1	0	0	0	1	0	0
vulcani	1	1	2	0	0	1	0	1	0	1	1	1	1	1	2	1	0	1	0	1	0	0	0	1	1	0
bisulcata	0	1	0	1	0	1	1	1	0	1	0	1	1	0	2	1	0	?	0	0	0	0	0	0	0	0
trentonenesis	0	1	0	1	0	1	1	1	0	1	0	1	1	1	2	1	0	0	0	0	0	0	0	1	0	0
arago	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1
vacuvertis	1	1	1	1	1	1	1	0	0	1	1	0	1	0	1	1	1	1	1	0	1	1	1	0	0	0
oehlerti	1	1	1	1	0	1	1	0	0	1	1	0	1	0	1	1	1	1	1	0	1	1	1	0	0	0
rouaulti	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1
boisselli	0	0	2	0	0	0	0	0	1	0	0	0	?	?	0	1	1	?	0	1	0	0	0	0	0	0
alcantarae	1	0	2	0	1	0	0	0	1	0	0	0	0	?	0	1	1	?	0	1	0	0	0	0	0	0
sdzuyi	0	0	0	0	1	?	?	0	1	0	1	0	?	?	0	1	0	?	0	0	0	1	0	0	0	0

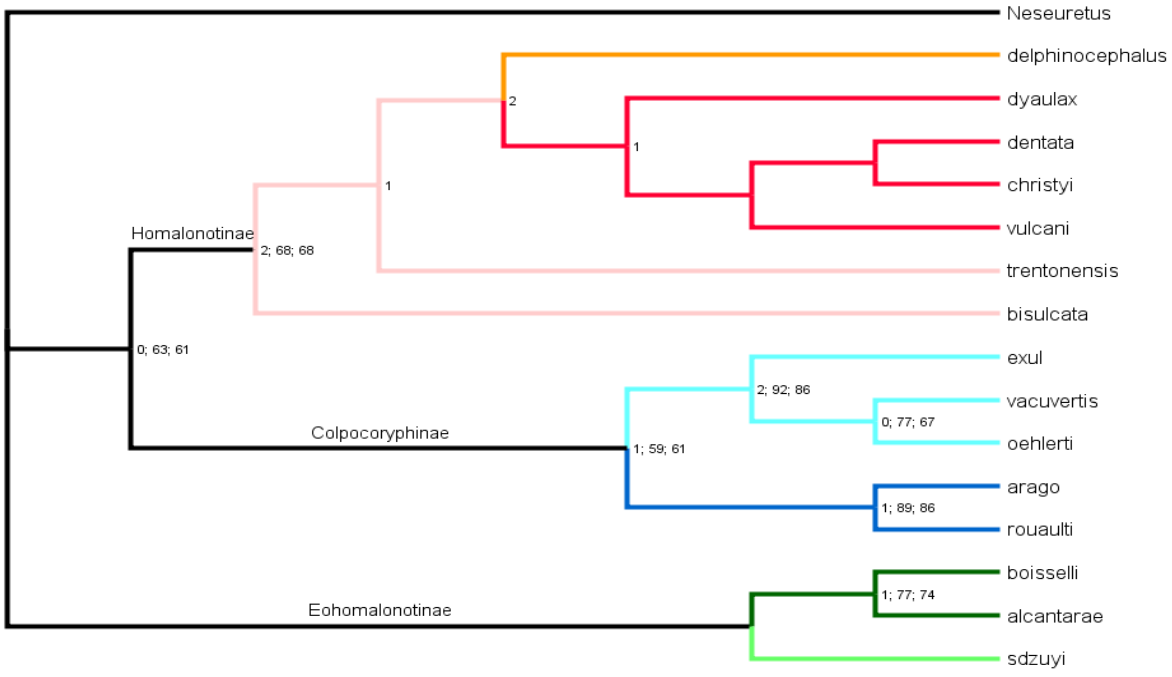

Fig 2: Cladogram of the results from the parsimony analysis. Tree graphics generated using FigTree v.1.1.2 (Rambaut 2008). The stems that connect to an end member species have been color coded based on the genus they were traditionally assigned to, where *Platycoryphe* is red, *Trimerus* is orange, *Brongniartella* is pink, *Plaesiacomia* is light blue, *Colpocoryphe* is dark

blue, *Calymenella* is dark green, and *Eohomalonotus* is light green. The values at the nodes are the results from the statistical tests. The first number is the Bremer Support value, the second is the Bootstrap value, and the third is the Jackknife value. Trees for the Bootstrap and Jackknife analyzes were generated using 50% majority rule consensus.

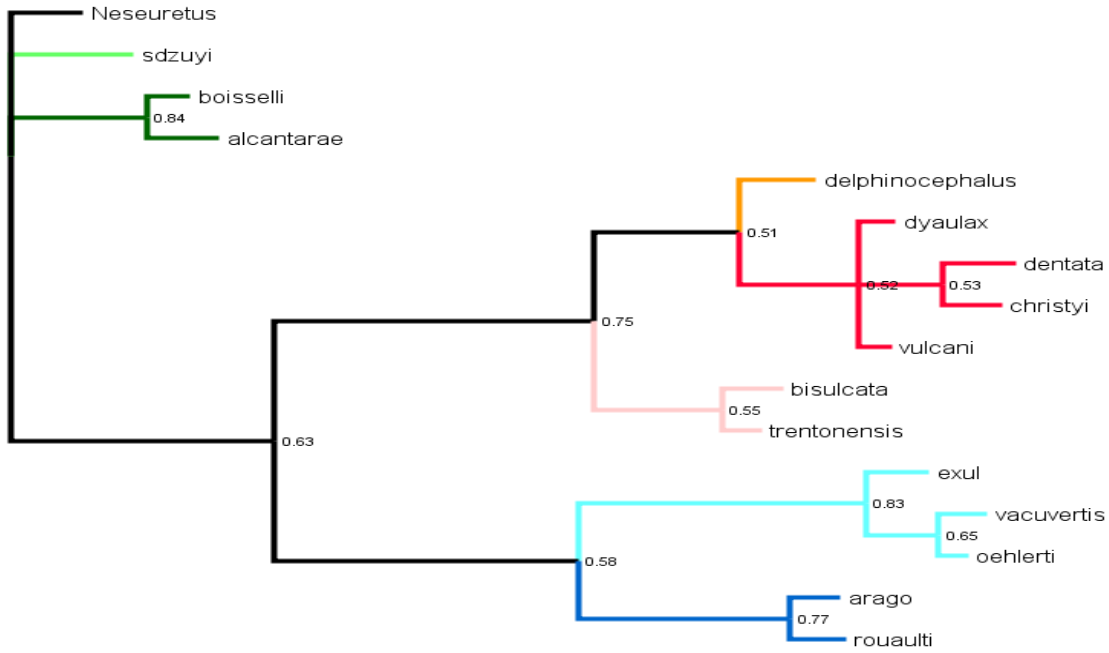

Fig 3: Phylogram of the results from the Bayesian analysis. Tree graphics generated using FigTree v.1.1.2 (Rambaut 2008]). The stems that connect to an end member species have been color coded based on the genus they were traditionally assigned to, where *Platycoryphe* is red, *Trimerus* is orange, *Brongniartella* is pink, *Plaesiacomia* is light blue, *Colpocoryphe* is dark blue, *Calymenella* is dark green, and *Eohomalonotus* is light green. The values at the nodes are the posterior probabilities for those nodes.

Results

Analysis results and comparison between phylogenetic methods- The parsimony analysis yielded the single most parsimonious tree with a length of 54, a CI of 0.5185, and an RI of 0.7615 (Fig. 2). The Bayesian analysis also yielded a tree, although none of the posterior probabilities were significant with 95% confidence (Fig. 3). The nodes with the highest posterior probabilities in the Bayesian analysis also had the highest Jackknife and Bootstrap values in the parsimony analysis. High Bremer support values, however, did not strongly correlate with high posterior probabilities; for instance, the node that defines a monophyletic group with *Trimerus* and *Platycoryphe* has a Bremer support value of 2, but a posterior probability of only 51%. Focusing on the topologies of both trees, the relationships implied by the parsimony tree basically concur with those implied from the Bayesian derived tree, with two exceptions. In particular, the Bayesian analysis predicted *Brongniartella* was monophyletic, while the parsimony analysis indicated *Brongniartella* was paraphyletic (in essence "giving rise" to both *Trimerus* and *Platycoryphe*). Further, the parsimony analysis indicated that *Eohomalonotus* grouped with *Calymenella*, while the Bayesian analysis placed both taxa in a polytomy. For the purposes of taxonomy and biogeography, I will be using the tree generated from the parsimony analysis as my phylogenetic hypothesis. The Bayesian tree can be treated as another means of gauging support for different aspects of the tree, in addition to the Jackknife/Bootstrap and Bremer support methods.

I chose to include members of the genus *Colpocoryphe* in my analysis despite Henry's (1980) claim that the genus belongs to the Calymenidae based on hypostomal characters. I found that *Colpocoryphe* grouped with the ingroup and close to *Plaesiacomia*, which challenges aspects of Henry's (1980) hypothesis; however, I was unable to include hypostomal characters given their typically poor and incomplete state of preservation. In order to test how strongly the presence of *Colpocoryphe* affected the tree topology, all members of the genus were removed and the data matrix was analyzed again. The absence of *Colpocoryphe* had no affect on the topology. Henry (1980) also argued *Calymenella* was a calymenid. Again, my phylogenetic results do not support this contention, but to test the effect including this taxon had on my result, I removed *Calymenella* from the analysis: the overall topology did not change.

Systematic Paleontology- According to my analysis *Calymenella*, *Colpocoryphe*, *Plaesiacomia* and *Platycoryphe* are monophyletic. Therefore, I do not redefine these taxa. *Brongniartella* as traditionally conceived is paraphyletic. Since *bisulcata* is the type species, I suggest that it be placed in a monotypic genus *Brongniartella*. Using the convention established by Wiley (1978), I place *trentonensis* in "*Brongniartella*", with the quote marks denoting the group's paraphyly. (I am hesitant to create a monotypic genus for *trentonensis* simply because I have not included every known taxa of "*Brongniartella*" and thus do not know the entire structure of this paraphyletic group.) It was impossible to determine if *Eohomalonotus* or *Trimerus* as traditionally

conceived were monophyletic since I only included one species of each of these taxa, and my primary emphasis was on Ordovician and Early Silurian exponents of the homalonotids.

The data suggests three larger monophyletic groups (subfamilies) within the Homalonotidae: one consisting of *Trimerus*-"*Brongniartella"*-*Platycoryphe*; another consisting of *Colpocoryphe*-*Plaesiacomia*; and the third consisting of *Eohomalonotus*-*Calymenella*. These subfamilies on the whole match those Thomas (1977) identified. In particular, Thomas (1977) grouped *Trimerus*, *Brongniartella*, and *Platycoryphe* within the Homalonotinae; he grouped *Colpocoryphe* and *Plaesiacomia* within the Colpocoryphinae Hupé, 1955; and he grouped *Calymenella* and *Eohomalonotus* within the Eohomalonotinae Hupé, 1953. Since my data supports Thomas's (1977) revision of these subfamilies, no new redefinition of these groups is required.

Genus **BRONGNIARTELLA** Reed 1918

TYPE SPECIES: *Homalonotus bisulcata* M'Coy 1851, ex Salter, MS.

DISCUSSION: Since the genus *Brongniartella* has been shown to be paraphyletic, I redefine the genus into a monotypic genus that includes only its type species, *bisulcata*, and refer the other species considered to the paraphyletic "*Brongniartella*". For an in-depth diagnosis of *Brongniartella bisulcata*, refer to Dean (1961).

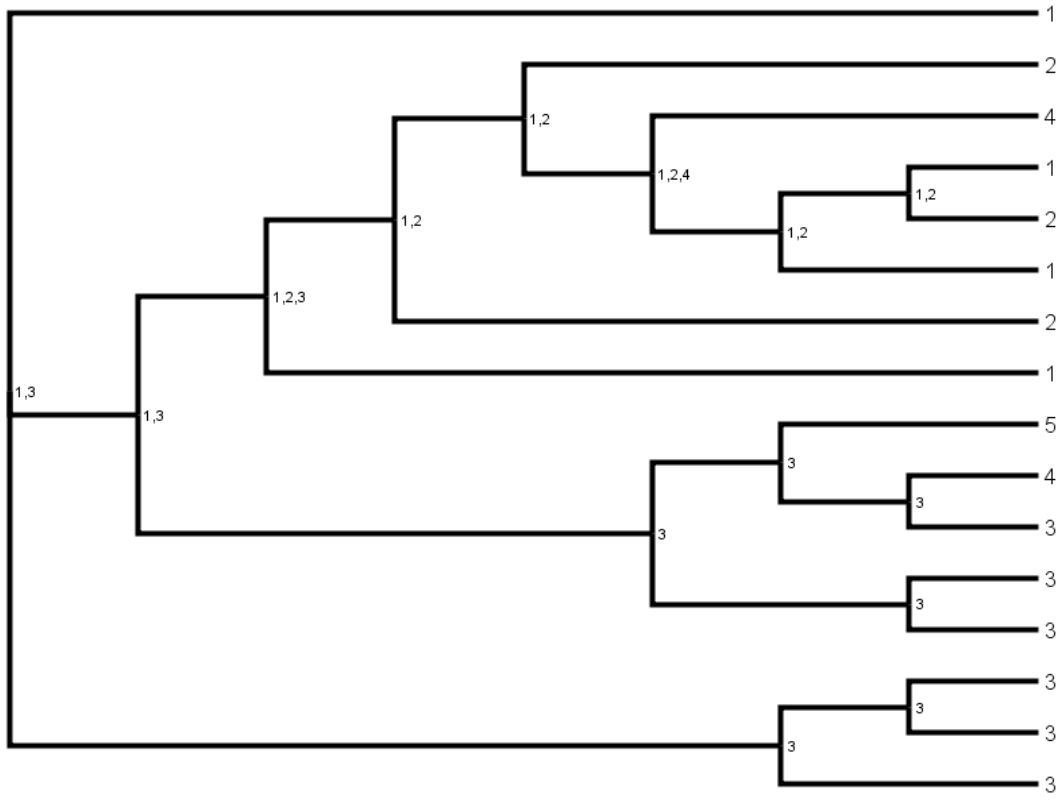

Fig 4: Area cladogram. Tree graphics generated using FigTree v.1.1.2 (Rambaut 2008). The numbers code for the locations in which the taxa were found, where *1* = Avalonia, *2* = E. Laurentia, *3* = Armorica, *4* = Arabia, and *5* = Florida. The numbers at the nodes are the optimized locations of the ancestral taxa.

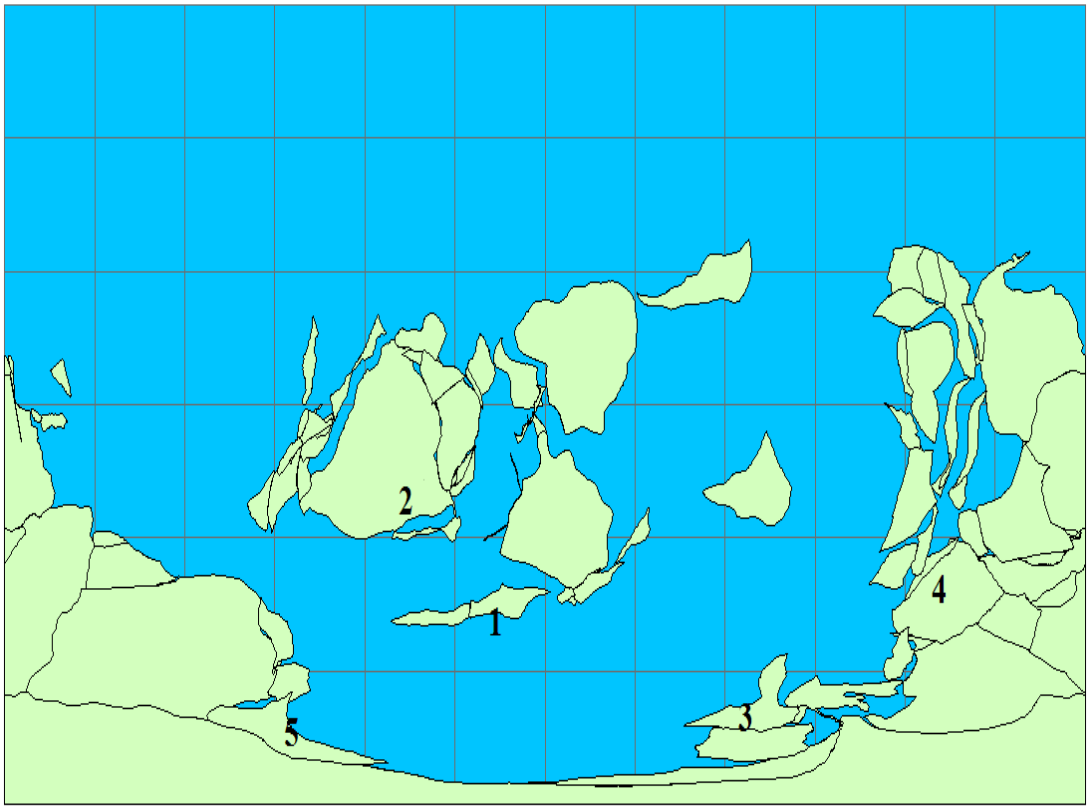

Fig 5: Map of the late Ordovician (Caradoc) world generated with ArcView 9.2 and PaleoGIS (Scotese 2007). The biogeographic areas used in this analysis are numbered *1* = Avalonia, *2* = E. Laurentia, *3* = Armorica, *4* = Arabia, and *5* = Florida.

Biogeography Analysis: Methods- I used my phylogeny to perform a biogeographic analysis using a modified version of Brooks parsimony analysis (BPA). This method is described in detail in Lieberman and Eldredge (1996), and Lieberman (2000, 2003), although some brief discussion is provided here, and has been used successfully to investigate biogeographic patterns in a variety of groups, including

trilobites, e.g. Lieberman and Eldredge (1996), Lieberman (2000), Hembree (2006), Rode and Lieberman (2005), and Lee et al. (2008). BPA is discussed in detail in (Brooks et al., 1981; Brooks, 1985; and Wiley, 1988). Modified BPA makes it possible to detect patterns of geodispersal and vicariance. First, I created an area cladogram by replacing the names of the end member taxa with the geographic areas in which these taxa were found (Fig. 4). The areas used in the analysis were Avalonia (Newfoundland and Great Britain), Eastern Laurentia (the United States), Armorica (France and Spain), Arabia (Saudi Arabia), and Florida (Fig. 5) These areas were defined on the basis of geological evidence and because they contain large numbers of endemic taxa; in effect this follows the area descriptions and designations of Fortey and Cocks (1992), Scotese and McKerrow (1991), Harper (1992), Torsvik et al (1995) and Torsvik et al (1996). Next, the geographic locations for the ancestral nodes of the area cladogram were optimized using a modified version of the Fitch (1971) parsimony algorithm. Then, the area cladogram was used to generate two matrices, one to code for patterns of vicariance and the other to code for patterns of geodispersal. The former provides information about the relative time that barriers formed, isolating regions and their respective biotas; the latter provides information about the relative time that barriers fell, allowing biotas to congruently expand their range (Lieberman and Eldredge 1996; Lieberman 2000, 2003). Each matrix was then analyzed using an exhaustive search on PAUP 4.0 (Swofford 1998). The results are presented in Figure 6. All matrix data was compiled into Nexus files using Mesquite

v.2.01 (Maddison and Maddison 2007) and trees were generated using FigTree v.1.1.2 (Rambaut 2008).

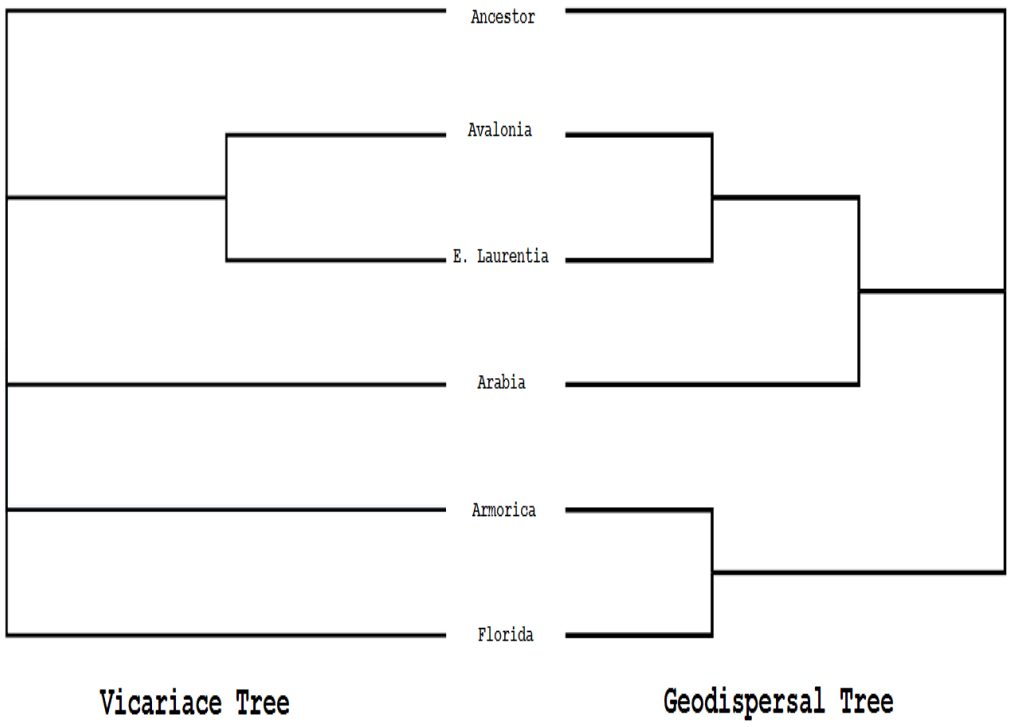

Fig 6: On the right the most parsimonious geo-dispersal tree and on the left the strict consensus of four most parsimonious vicariance trees.

Results of the biogeographic analysis- The geodispersal analysis yielded the single most parsimonious tree of 37 steps. The tree suggests the most recent barriers to fall were those between E. Laurentia and Avalonia and those between Florida and Armorica. The next most recent barriers to fall were those between a combined E. Laurentia-Avalonia and Arabia. Finally, the oldest barriers were those between E.

Laurentia-Avalonia-Arabia and Florida-Armorica. The vicariance analysis yielded four most parsimonious trees of 47 steps. A strict consensus of these four trees has only one resolved node: Avalonia and E. Laurentia, suggesting some vicariance between trilobites from these respective regions.

I also used the test of Hillis (1991), the g_1 statistic, to see whether the results from my analysis differ from those produced using random data. My results differ from those generated using random data at the .01 level. Bootstrap, Jackknife, and Bremer support values were calculated for both trees. In the geodispersal tree, the node uniting Avalonia and Laurentia was most robust, with Bremer, Bootstrap, and Jackknife values of 2, 91%, and 87% respectively. In the vicariance tree, the node uniting Avalonia and Laurentia had Bremer, Bootstrap, and Jackknife values of 3, 95%, and 92% respectively.

Interpretation of biogeographic results and discussion- The close relationship between E. Laurentia and Avalonia is replicated in both the vicariance and geodispersal trees (Fig. 4). This suggests that the processes producing vicariance and geodispersal between these areas were similar, implicating cyclical processes, likely sea-level rise and fall, played an important role in generating the biogeographic patterns (Lieberman and Eldredge 1996; Lieberman 2000, 2003; Rode and Lieberman 2005). In effect, this result largely matches paleomagnetic and tectonic evidence which indicates that Avalonia rifted from Gondwana during the early-mid Ordovician and began drifting towards Laurentia and Baltica; during the early Silurian, Avalonia

and Baltica joined together to form Balonia; and this in turn collided with Laurentia during the Taconic orogeny (Trench and Torsvik 1992, Soper et al 1987; McKerrow 1988; Scotese and McKerrow 1991, Torsvik et al 1996). Probably by the late Ordovician the Iapetus Ocean was effectively closed (Trench and Torsvik 1992). My data suggest that either Laurentia and Avalonia were geographically close enough to each other during the late Ordovician to directly exchange taxa when sea level rose sufficiently, or they were indirectly exchanging taxa, with Baltica acting as an intermediary.

My results, in particular, the geodispersal tree (Fig. 6), also indicate a close biogeographic relationship between Avalonia-Laurentia and Arabia. When the patterns implied by the vicariance and geodispersal trees differ, as is the case with this aspect of the biogeographic results, it could be due to a tectonic collision or a chance long distance dispersal event (Lieberman and Eldredge 1996; Lieberman 2000, 2003; Rode and Lieberman 2005). Given that there is no substantial tectonic evidence linking these regions, the dispersal between Avalonia-Laurentia and Arabia was unlikely to have been facilitated by a tectonic event, and instead may have been due to chance long distance dispersal between these regions. This dispersal could have been facilitated by a planktonic larval stage, however homalonotids are presumed to have had benthic larvae (*sensu* Speyer and Chatterton 1989). Dispersal also could have been facilitated by chains of island arcs that allowed organisms to island-hop to Gondwana.

The geodispersal tree also shows a grouping of Armorica and Florida (Fig. 6). During the late Ordovician, paleomagnetic and tectonic evidence suggests that Armorica had rifted away from the main continent of Gondwana (Trench and Torsvik 1992, Torsvik et al 1996). It is possible the rifted Armorica could have moved close enough to Florida to exchange taxa during this time period. However, since the vicariance tree does not record this rifting event, I cannot be sure if the separation of Armorica from Gondwana had the primary affect on the biogeographic patterns of homalonotids at the time, or instead these patterns were due to chance long distance dispersal. Furthermore, again there is no strong tectonic evidence to support a collision between Florida and Armorica.

My area cladogram (Fig. 4) also indicates that the homalonotids most likely originated in Gondwana, during a time when Avalonia was still connected to the main continent. This is because the area of the ancestral node of all homalonotids consists of a united Avalonia and Armorica. If we track patterns of biogeographic change up the tree, it appears that Avalonia then rifted from Gondwana, carrying with it a homalonotid fauna that diversified in Avalonia and later dispersed from Avalonia into Laurentia. My data indicates Laurentian homalonotids have a close evolutionary relationship with Avalonian forms. Indeed, all Laurentian and Avalonian homalonotids group in a single subfamily (Figs. 2, 4). Ultimately, the movement of homalonotids into Laurentia appears to have had an important effect on macroevolutionary patterns in the group, as the group underwent substantial subsequent diversification after it entered that region.

Phylogeny and biogeography of deiphonine trilobites

Introduction

The Cheiruridae Hawle and Corda 1847 are a diverse family of phacopine trilobites that originated in the earliest Ordovician and persisted until the Devonian. Members of the group are characteristically spinose and are diagnosed by unique hypostomal and pygidial characters. Although the group is widely believed to be monophyletic, evolutionary relationships within the cheirurids are largely unknown since there have been few phylogenies generated for the group (see Adrain 1998 for an example of one such study). Lane (1971) is the most recent taxonomic revision of the group, and he recognized seven subfamilies within the cheirurids. One of these subfamilies is the Deiphoninae Raymond 1913, a group diagnosed by a spherical inflation of the glabella past the S1, a rectangular hypostome, and the retention of the last pygidial segment throughout ontogeny. Deiphonine trilobites originated in the middle Ordovician and persisted into the Silurian.

The primary purpose of this paper is to use phylogenetic methods to construct a hypothesis of relationship for the group Deiphoninae, as part of a broader investigation of evolutionary patterns within the entire Cheiruridae. The second purpose of this paper is to study the effects of the end Ordovician mass extinction event on these trilobite taxa. Since deiphonine trilobites straddle the Ordovician-Silurian boundary they are potentially important taxa for use in studying the evolutionary and biogeographic effects of the mass extinction. In this paper, I use my

hypothesis of relationship to explore the evolutionary patterns of the Deiphoninae during the extinction event. Furthermore, I use this phylogenetic hypothesis to reconstruct biogeographic patterns in the group by conducting a modified Brooks Parsimony Analysis (see Lieberman and Eldgredge 1996; Lieberman 2000). This analysis allows us to ascertain the extent to which biogeography played a role in survival during the end Ordovician mass extinction.

Materials

Specimens were analyzed from the Yale Peabody Museum, the Museum of Comparative, the Field Museum, and the University of Iowa.

Methods

Morphological terminology follows Whittington et al. (1997).

Taxa analyzed.—A total of twenty-one taxa were included in the analysis. *Actinopeltis* Hawle and Corda 1847 was chosen as the outgroup since it is most likely sister group to the Deiphoninae. Although the genus has sometimes been placed in other subfamilies, including the Cheirurinae Hawle and Corda 1847 and Cyrtometopinae Öpik 1937 (see Lane 1971 and Moore 1959 respectively), its affinities lie with Deiphoninae because it possesses a similarly bulbous glabella and lacks the thorasic pleural furrows found in members of Cheirurinae. Members of the ingroup were originally placed within *Sphaerocoryphe* Angelin 1854, *Deiphon* Barrande 1850, and *Onycopyge* Woodward 1880. *Onycopyge* is a monotypic genus

found only in Australia. The original holotype specimen was so poorly preserved that Lane (1971) argued against the genus being placed within the Cheiruridae. However, new material described by Holloway and Campbell (1974) clearly showed that the taxon is a deiphonine cheirurid. One taxa included in this analysis, *Sphaerocoryphe elliptica* Zhou, Dean, Yuan, and Zhou 1998, was considered by Zhou to have possible affinities with the genus *Hemisphaerocoryphe* Reed 1896. A few other taxa have been referred to *Hemisphaerocoryphe* but these could not be considered in the present phylogenetic analysis because either they were too poorly preserved and incomplete or the relevant material could not be obtained.

Characters.—The majority of the characters used in phylogenetic analysis come from the dorsal side of the mineralized exoskeleton. Only one hypostomal character was used because deiphonine trilobites have little variation in hypostomal morphology. The characters are listed below in approximate order from anterior to posterior position on the organism. A complete character matrix is given in Table 2.

Cephalon

1. Ocular ridges - a: run directly into the lateral glabellar furrow, b: are separated from the glabella by a small field.
2. Posterior margin of the glabella - a: straight, b: convex.
3. Glabella length/width - a: glabella wider (tr.) than long (sag.), b: glabella longer (sag.) than wide (tr.), c: glabellar length (sag.) equals glabellar width (tr.).

4. Convexity of the anterior part of the glabella (lateral view) drawing a dorsal line that runs tangential to the glabella, the angle made by the curving of the glabella as it curves ventrally with respect to the horizontal line - a: 10-20°, b:35-40°.
5. Genal spines - a: curved posteriorly (distal margins strongly convex), b: straight (distal margins weakly convex).
6. S1 - a: strongly incised, b: reduced or absent.
7. Occipital ring - a: parallel to thoracic axis medially, with posteriorly directed wing-like processes at the lateral ends, b: curved anteriorly.
8. S2 - a: present, b: absent or indistinct.
9. Terminal tip of genal spine - a: curves ventrally, b: remains flat.
10. Glabellar sculpture - a: lightly granulated, b: densely granulated.
11. Genal spine length (exsag.) - a: stubby (<= the width tr. of the occipital ring) b:elongate (>= 1.4x the width tr. of the occipital ring).
12. Genal spine departs from the cephalon - a: between 30-60° from the sagittal, b: at approximately 90° from the sagittal.
13. Number of sets of spines on the librigena - a: 1, b: 2.

Hypostome

14. Middle body shape - a: subquadrate, b: subovate.

Thorax

15. Sculpture of segments - a: densely granulated, b: lightly granulated.
16. Pleurae furrows - a: possess furrows, b: lack furrows.
17. Tips of pleurae - a: rounded, b: pointed.

Pygidium (Pygidial spines are grouped as 1st, 2nd, and 3rd, with 1st coming off the first axial ring, second from the next, and so on.)

18. Pygidial fork, a: visible in dorsal view - b: not visible in dorsal view.
19. Posterior pygidial margin convexity (lateral view) - a: prominent, b: absent.
20. pygidial spine structure - a: simple (ratio of width proximal to width medial ~ 1), b: triangular (ratio of width proximal to width medial >> 1).
21. Pygidial sculpture (dorsal) - a: densely granulated, b: lightly granulated.
22. 1st spine, a: longer (exsag.) than second spine, b: shorter (exsag.) than 2nd spine or indistinct.
23. Condition of 2nd spine set - a: converges at the pygidial axis into an expanded shield that covers the first axial ring and the posterior pygidial margin, b: connects to the second axial ring without forming a pygidial shield.
24. 2nd spine set leaves pygidial axis at - a: 30-50 degrees from sagittal, b: 80-90 degrees from sagittal.
25. 2nd set of pygidial spines width (measured exsagittally where the spine leaves the pygidium) - a: wide (width [exsag.] > twice length [sag.] 1st axial ring), b:

thin (width [exsag.] significantly < twice length [sag.] 1st axial ring) or reduced.

26. 1st spine set leaves pygidial axis at - a: 30-50 degrees from sagittal, b: 80-90 degrees from sagittal.
27. 1st pygidial spine set width (measured exsagittally where the spine leaves the pygidium), a: wide (width [exsag.] significantly > length [sag.] 1st axial ring), b: thin (width [exsag.] < length [sag.] 1st axial ring).
28. distal end of pygidial spines a: rounded, b: pointed.
29. Medial parts of 2nd pygidial spine sets, a: roughly parallel sagittal line, b: oblique to sagittal
30. Distal end of 2nd spine set a: curved abaxially, b: curved adaxially, c: pointed straight posteriorly.
31. Medial part of 1st spine set a: roughly parallel to transverse line, b: oblique to transverse.
32. Distal end of 1st spine set a: curved abaxially, b: curved adaxially, c: pointed straight posteriorly.
33. 3rd spine a: absent, b: present.

Table 2: Deiphonine character matrix

taxa/characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
globosa	b	a	b	a	b	a	b	a	b	a	a	a	?	?	b	b	?	b	a	a	b	a	b	b	a	b	b	a	b	a	a	a	b
carolialexandri	b	a	b	a	b	a	b	a	b	a	a	a	?	?	b	b	b	b	a	b	b	a	b	b	b	b	a	b	b	c	a	b	b
goodnovi	b	a	b	a	a	a	b	b	b	b	b	a	a	b	b	b	a	b	a	b	a	b	b	a	b	b	a	a	b	a	b	b	a
barrandei	a	a	a	b	a	b	a	b	b	b	b	a	a	a	b	b	b	b	b	b	b	b	a	a	a	a	a	b	b	c	b	a	a
globifrons	a	a	a	a	a	b	a	b	a	b	b	a	a	a	b	a	b	b	b	b	b	b	a	a	a	a	a	b	b	b	b	a	a
ellipticum	a	b	c	a	a	b	a	b	?	b	b	b	a	a	a	a	b	b	b	b	b	b	a	a	b	a	a	b	b	c	b	b	a
liversidgei	b	b	a	?	a	b	b	b	b	b	b	a	b	?	?	b	b	a	a	a	a	a	b	a	a	b	b	a	a	b	b	b	a
bainsi	a	b	a	?	b	b	a	b	a	b	b	b	a	a	b	b	a	b	b	a	a	?	a	a	b	a	a	b	b	a	b	a	a
grovesi	a	b	c	a	a	b	a	b	a	b	b	b	a	a	?	?	?	b	b	a	a	a	a	a	b	a	b	a	b	a	b	b	a
robustus	b	a	b	b	a	a	b	b	b	a	b	a	a	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	b	a	b	a	a
kingi	b	a	b	?	b	a	b	b	?	a	a	a	b	?	b	b	b	b	b	b	?	b	?	b	a	b	b	?	b	a	a	a	a
dentata	b	a	b	b	b	a	b	b	b	a	a	a	b	b	b	b	b	b	a	b	b	b	b	?	a	b	a	a	b	a	a	b	a
longispina	b	a	b	?	b	a	b	b	a	b	a	a	a	b	?	?	?	b	b	b	a	?	b	b	a	b	?	b	b	c	?	?	a
gemina	b	a	b	a	b	a	b	b	b	b	a	a	a	b	?	?	?	b	a	b	a	b	b	b	b	b	a	a	b	c	a	b	a
cranium	b	a	b	b	b	a	b	b	b	a	a	a	?	?	b	b	b	b	b	b	b	b	b	b	a	b	a	b	a	b	a	b	b
longifrons	a	a	b	b	a	b	a	b	a	b	b	b	a	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
maquoketensis	b	a	b	b	a	a	b	b	a	a	b	a	a	?	b	b	?	b	b	b	b	b	b	b	a	b	?	?	b	a	?	?	a
S. elliptica	a	a	b	a	b	a	b	a	b	a	a	a	?	?	a	b	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
murphyi	b	a	b	?	?	a	?	b	?	a	?	a	b	b	?	?	?	b	b	b	a	b	b	b	b	b	a	b	b	a	a	b	a
exserta	b	b	c	?	a	b	b	b	a	a	b	a	a	?	?	?	?	a	a	a	a	b	b	b	b	b	a	a	b	a	a	b	a
fleur	a	a	a	a	?	b	a	b	?	b	?	b	a	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Phylogenetic analysis.—The data were analyzed using TNT v1.1 (Goloboff, Farris, Nixon 2008). An implicit enumeration was used to determine the most parsimonious trees for this data matrix. All multistate characters were treated as unordered. Bootstrap, Jackknife, and Bremer (1990) support values were calculated using TNT v1.1 (Goloboff et al. 2008). Bootstrap and Jackknife tests were analyzed heuristically using 100 replicates. All matrix data was compiled into Nexus files using Mesquite v.2.01 (Maddison and Maddison 2007) and trees were generated using FigTree v.1.1.2 (Rambaut 2008).

Specific taxa analyzed.—*Sphaerocoryphe goodnovi* Raymond 1905, *S. exserta* Webby 1974, *S. gemina* Trip, Rudkin and Evitt 1997, *S. robusta* Shaw 1968, *S. cranium* (Kutorga 1854), *S. kingi* Ingham 1974, *S. murphyi* Owen, Tripp and Morris 1986, *S. longispina* Trip, Rudkin and Evitt 1997, *S. maquoketensis* Slocom 1913, *S. dentata* Angelin 1854, *S. elliptica* Zhou, Dean, Yuan, and Zhou 1998, *Deiphon barrandei* Whittard 1934, *D. globifrons* Angelin 1854, *D. longifrons* Whittard 1934, *D. fleur* Snajdr 1980, *D. ellipticum* Ramsköld 1983, *D. braybrooki bainsi* Chatterton and Perry 1984, *D. grovesi* Chatterton and Perry 1984, and *Onycopyge liversidgei* Woodward 1880 for a total of nineteen ingroup taxa. *Actinopeltis globosa* Whittington 1968 and *A. carolialexandri* Hawle and Corda 1847 were used as outgroups.

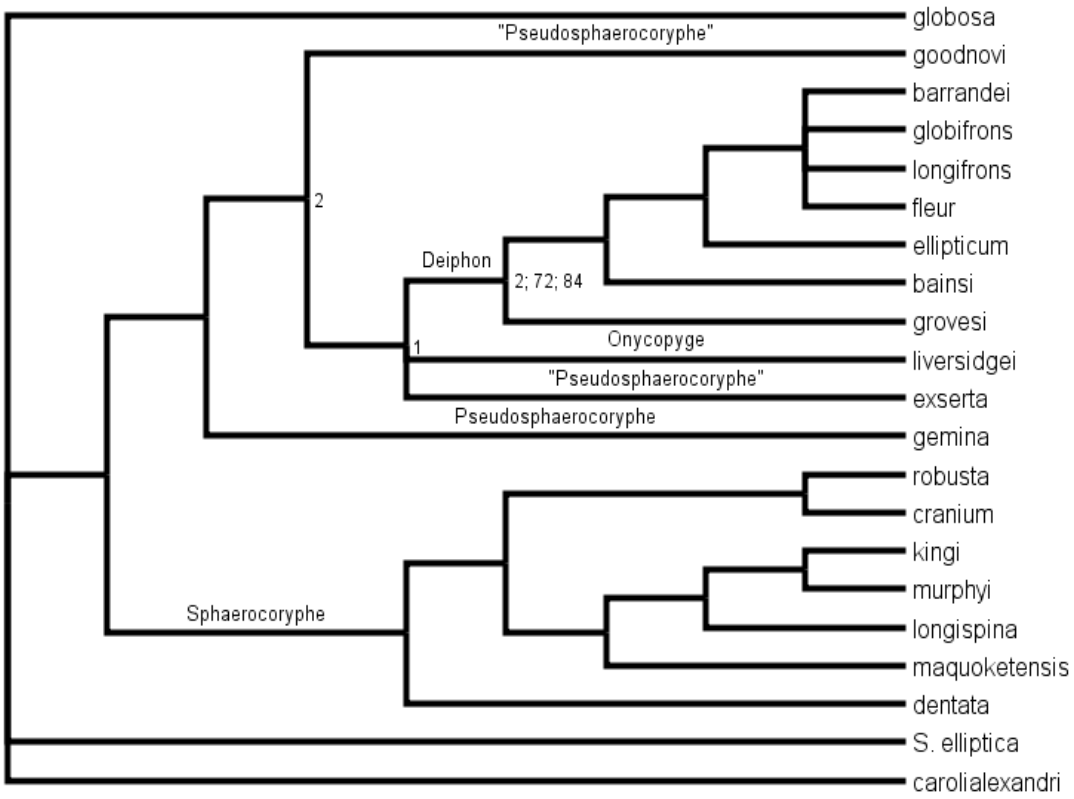

Fig 7: Cladogram of the strict consensus of my results from the parsimony analysis. Tree graphics generated using FigTree v.1.1.2 (Rambaut 2008). The nodes that define a genus have been labeled with the generic name. Using the convention of Wiley (1978), paraphyletic groups are identified using quote marks. The values at the nodes are the results from the statistical tests. The first number is the Bremer Support value, the second is the Bootstrap value, and the third is the Jackknife value. Trees for the Bootstrap and Jackknife analyzes were generated using 50% majority rule consensus.

Results

Phylogenetic analysis produced four most parsimonious trees of length 89. Each tree had an RI value of 0.679 and a CI value of 0.404. A strict consensus of all four trees is shown in figure 7. My analysis suggests two major lineages within the Deiphoninae. One lineage, which goes extinct at the end Ordovician, contains only taxa originally assigned to *Sphaerocoryphe*. The other lineage, which continues on into the Silurian, contains a few taxa originally assigned to *Sphaerocoryphe*, as well as taxa originally assigned to *Deiphon* and *Onycopyge*. This suggests that there is a monophyletic clade nested within a paraphyletic *Sphaerocoryphe*. *Sphaerocoryphe* (*Hemisphaerocoryphe*?) *elliptica* grouped with the outgroup, *Actinopeltis*, suggesting that it is part of a separate lineage and not truly part of the Deiphoninae.

Systematic paleontology.—My analysis shows that the genera *Deiphon* and *Onycopyge* as originally defined are monophyletic. *Sphaerocoryphe* as traditionally defined was paraphyletic; therefore I advocate that the species *gemina, goodnovi, exserta* and *elliptica* be removed from the genus so that *Sphaerocoryphe* can be made into a true monophyletic group that includes its type species, *S. dentata*. I suggest that a new monotypic genus, *Pseudosphaerocoryphe*, be erected with the type species *P. gemina* Tripp, Rudkin, and Evitt 1997. Using the convention of Wiley (1978), I place the species *goodnovi* and *exserta* in the group "*Pseudosphaerocoryphe*", with the quotes denoting paraphyly. (I am hesitant to create monotypic genera for both species because I have not included every species originally assigned to

Sphaerocoryphe in this analysis, and therefore I do not know the entire structure of this paraphyletic group).

It is important to note that, early on in the history of these two deiphonine lineages, it is difficult to define by traditional taxonomy whether a species belongs within the *Sphaerocoryphe* lineage or whether it is "on the line" to *Deiphon* (a member of the newly formed "*Pseudosphaerocoryphe*"). The divergence between these two lineages can only be ascertained by composite characters; in particular the light granulation of the glabella, the weak anterior convexity of the glabellar bulge, and the wide 2nd set of pygidial spines. If this phylogenetic hypothesis is true, then it suggests an interesting evolutionary scenario in which taxa that lived in the same area and shared similar morphological characters, like *gemina* and *longispina*, actually had completely disparate evolutionary trajectories. The descendants of *longispina* would go extinct at the end Ordovician, while the lineage of *gemina* would survive and persist into the Silurian.

I tentatively suggest that the taxon traditionally referred to as *Sphaerocoryphe* (*Hemisphaerocoryphe*?) *elliptica* be placed within the genus *Actinopeltis* based on the presence of the L2 glabellar furrow, which is absent in *Sphaerocoryphe* but present in *Actinopeltis*. However, since the type specimen of *elliptica* lacks a pygidium, new material will need to be described in order to fully ascertain if *elliptica* does indeed belong within *Actinopeltis*.

Family CHEIRURIDAE Hawle and Corda 1847

Subfamily DEIPHONINAE Raymond 1913

Genus PSEUDOSPHAEROCORYPHE new genus

Type Species.—*Sphaerocoryphe gemina*

Diagnosis.—Refer to Tripp et al. (1997) for their diagnosis of *Sphaerocoryphe gemina*.

Etymology.—The prefix pseudo- is attached to the generic name *Sphaerocoryphe* to indicate that members of this genus appear similar to *Sphaerocoryphe* but are part of a different monophyletic group that contains *Deiphon*.

Discussion.—Since several taxa originally diagnosed as *Sphaerocoryphe* were shown not to group within the monophyletic *Sphaerocoryphe*, I propose the creation of a new monotypic genus, *Pseudosphaerocoryphe* n. gen., which contains the taxon originally defined as *Sphaerocoryphe gemina*. The taxa *exserta* and *goodnovi* are referred to the paraphyletic group "*Pseudosphaerocoryphe*".

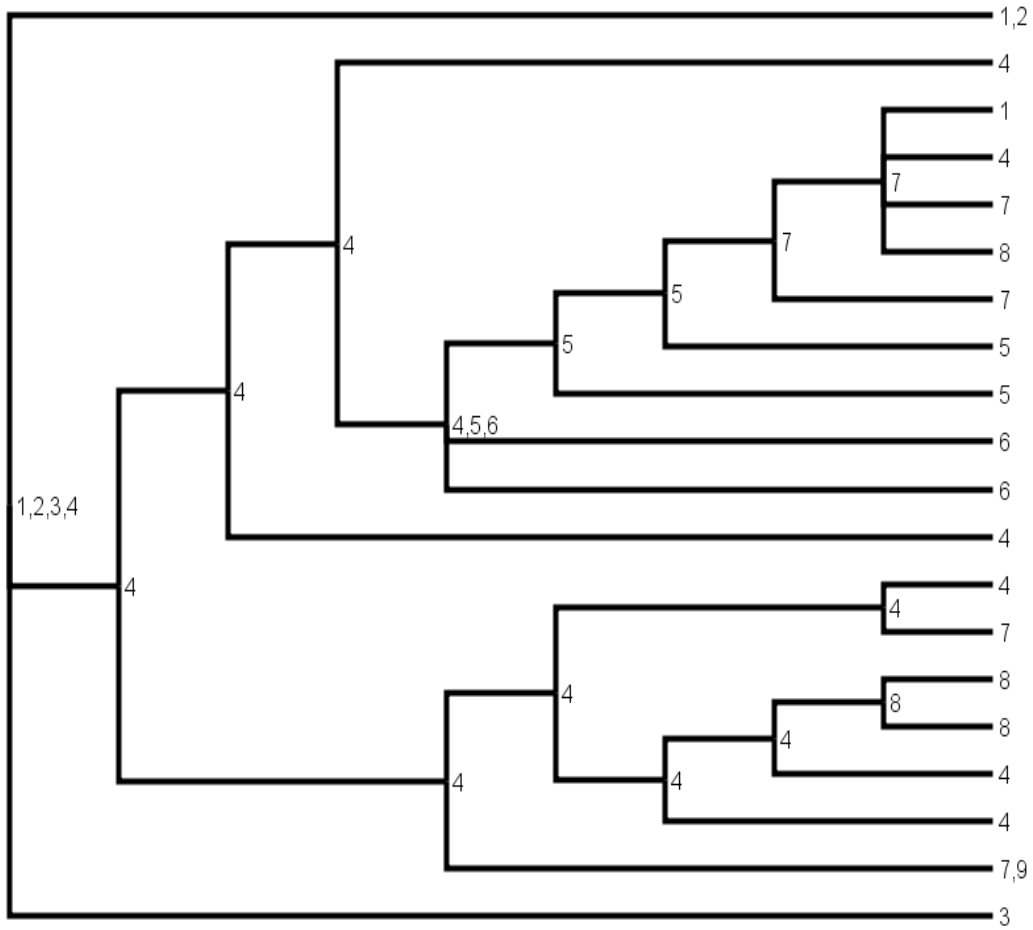

Fig 8: Area cladogram. Tree graphics generated using FigTree v.1.1.2 (Rambaut 2008). The numbers code for the locations in which the taxa were found, where *1* = Bohemia, *2* = Armorica, *3* = Tarim Plate, *4* = Eastern Laurentia, *5* = Northwestern Laurentia, *6* = Australia, *7* = Baltica, *8* = Avalonia, and *9* = Scotland. The numbers at the nodes are the optimized locations of the ancestral taxa.

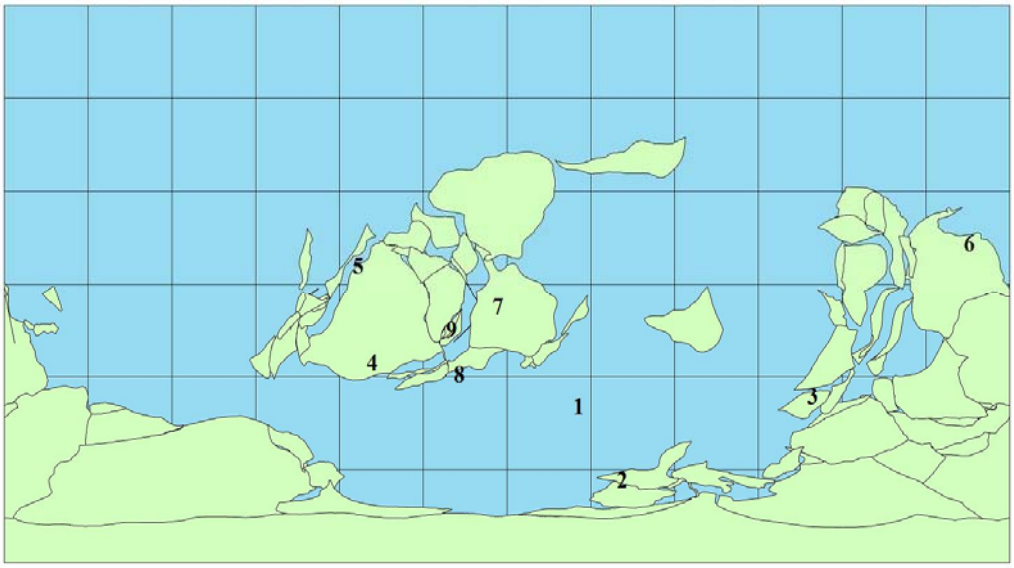

Fig 9: Map of the late Ordovician-early Silurian world generated with ArcView 9.2 and PaleoGIS (Scotese 2007). The biogeographic areas used in this analysis are numbered *1* = Bohemia, *2* = Armorica, *3* = Tarim Plate, *4* = Eastern Laurentia, *5* = Northwestern Laurentia, *6* = Australia, *7* = Baltica, *8* = Avalonia, and *9* = Scotland.

Biogeographic Study

Methods.—The phylogeny was converted to an area cladogram and analyzed using a modified version of Brooks parsimony analysis (BPA). This method is described in detail in Lieberman and Eldredge (1996), and Lieberman (2000, 2003), but some brief discussion is provided here. It has been used successfully to investigate

biogeographic patterns in a variety of fossil taxa, e.g. Lieberman and Eldredge (1996), Lieberman (2000), Hembree (2006), Rode and Lieberman (2005), and Lee et al. (2008). BPA is discussed in detail in (Brooks et al., 1981; Brooks, 1985; and Wiley, 1988). Modified BPA makes it possible to detect congruent patterns of both vicariance and geodispersal. First, I created an area cladogram by replacing the names of the end member taxa with the geographic areas in which these taxa were found (Fig. 2). The areas used in the analysis were Avalonia (present day Great Britain and Ireland), Eastern and Northwestern Laurentia (North America), Armorica (present day France and Spain), Bohemia (Central Europe), the Tarim Plate (in Central Asia), Scotland (Midland Valley Terrane- Girvan), and Baltica (present day Norway, Sweden, Eastern Russia, and Finland) (Fig. 3). These areas were defined on the basis of geological evidence and because they contain large numbers of endemic taxa; in effect these definitions follows the area designations of Fortey and Cocks (1992), Scotese and McKerrow (1991), Harper (1992) Torsvik et al (1995), Zhou and Zhen (2008), and Torsvik et al (1996). Next, the geographic locations for the ancestral nodes of the area cladogram were optimized using a modified version of the Fitch (1971) parsimony algorithm. Then, the area cladogram was used to generate two matrices, one to code for patterns of vicariance and the other to code for patterns of geodispersal. The former provides information about the relative time that barriers formed, isolating regions and their respective biotas; the latter provides information about the relative time that barriers fell, allowing biotas to congruently expand their range (Lieberman and Eldredge 1996; Lieberman 2000, 2003). Each matrix was then

analyzed using the exhaustive search option of PAUP 4.0 (Swofford 1998). The results are presented in Figure 4. All matrix data was compiled into Nexus files using Mesquite v.2.01 (Maddison and Maddison 2007) and images of trees were generated using FigTree v.1.1.2 (Rambaut 2008).

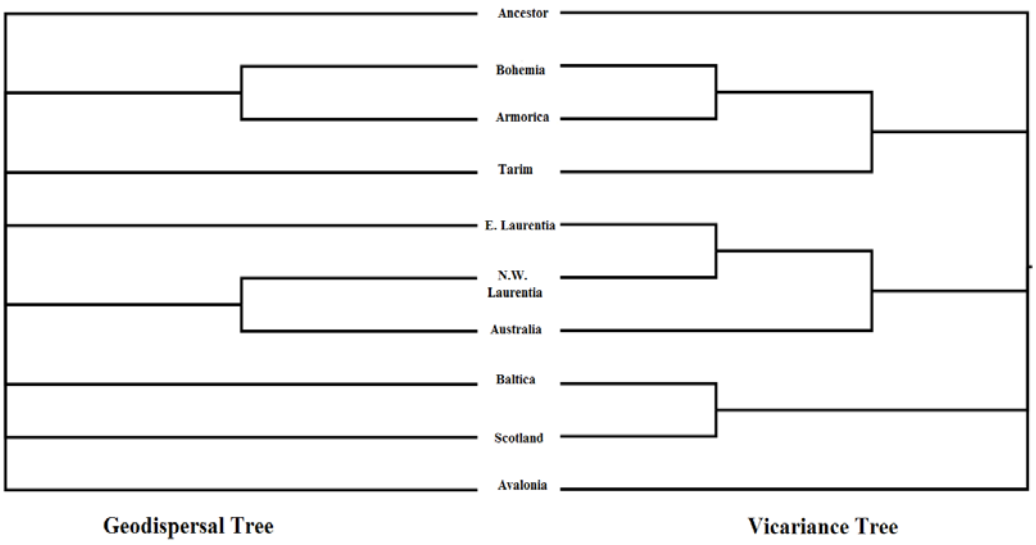

Fig 10: On the right the strict consensus of three most parsimonious geo-dispersal tree and on the left the most parsimonious vicariance tree.

Results of the analysis.—The geodispersal analysis yielded three most parsimonious tress of length 54 steps. A strict consensus of these trees has only two resolved nodes, one uniting Northwestern Laurentia and Australia, and the other uniting Bohemia and Armorica; this suggests that congruent geodispersal was limited and perhaps only took place between these two respective areas. The vicariance analysis has a most parsimonious tree of length 43 steps. The tree suggests that the most recent barriers to

form were between E. Laurentia and N.W. Laurentia, Baltica and Scotland, and Bohemia and Armorica. The next most recent barriers formed between a combined E. Laurentia-N.W. Laurentia and Australia, as well as between a combined Bohemia-Armorica and Tarim.

I used the test of Hillis (1991), the g_1 statistic, to see whether the results of my analysis would differ from those produced by random data. The g_1 statistics for the geodispersal and vicariance trees are -0.650820 and -0.685053 respectively. My results differ from those created by random data at the 0.01 level for both the geodispersal and vicariance matrices. Bootstrap and Jackknife values were calculated for both trees using a heuristic search with 100 replicates obtained via stepwise addition with random sequences of 100 replicates using the TBR algorithm. In the geodispersal tree, the nodes uniting N.W. Laurentia-Australia and Bohemia-Armorica were only resolved in the Bootstrap analysis and had values of .56 and .59 respectively. In the vicariance tree, the node uniting N.W. Laurentia-E. Laurentia-Australia had Bootstrap and Jackknife values of .69 and .68 respectively. The node uniting Tarim-Bohemia-Armorica had Bootstrap and Jackknife values of .80 and .66 respectively. The nodes uniting Baltica-Avalonia and Bohemia-Armorica were only resolved in the Bootstrap analysis and had values of .60 and .67 respectively.

Interpretation of results.—The close relationship between Bohemia and Armorica is shared in both the vicariance and geodispersal trees. This suggests that the processes affecting geodispersal and vicariance between these regions are similar (Lieberman 2000, 2003), thus implicating cyclical processes such as sea level rise and fall in

generating these biogeographic patterns. Therefore, my data suggests that these two landmasses were likely close enough to exchange taxa during the Ordovician. Tectonic and paleomagnetic data suggest that the Armorican and Bohemian massifs rifted from Gondwana independently. Bohemia rifted away from the southern continent during the middle Ordovician, while Armorica is believed to have been peripheral to Gondwana throughout the entire Ordovician (Tait et al. 1995, Torsvik et al 1996). The reason for this biogeographic grouping in my results largely appears to be determined by the presence of *Actinopeltis* in both of these areas during the early-late Ordovician. My vicariance tree also shows the formation of barriers between a combined Armorica-Bohemia and the Tarim plate. This vicariance was most likely caused by the early rifting of the two massifs from mainland Gondwana.

My data also suggests a close area relationship between Australia and Northwestern Laurentia, particularly in the geodispersal tree. My vicariance tree shows a close relationship between Eastern Laurentia and Northwestern Laurentia, as well as between a combined E. Laurentia-N.W. Laurentia and Australia. When the area relationships implied by the vicariance and geodispersal trees differ, it suggests that non-cyclical processes such as tectonic collision or long-range dispersal are responsible for the observed patterns. Given that there is no tectonic or paleomagnetic evidence to suggest a connection between Australia and Laurentia at this time, a collision between these areas seems unlikely and therefore I consider a long distance dispersal event by these cheirurid trilobites to be a more likely scenario, probably between a combined Eastern Laurentia-Northwestern Laurentia and Australia.

Subsequent to this dispersal event, vicariance occurred between Eastern and Northwestern Laurentia.

My vicariance tree also shows a close relationship between Baltica and the Midland Valley Terrane of Scotland. This close relationship is not replicated in my dispersal tree. Paleomagnetic and faunal studies suggest that the Midland Valley Terrane stayed peripheral to Laurentia throughout the Ordovician (Armstrong & Owen 2001; Torsvik et al 1996). Since there is no tectonic evidence to connect the Midland Valley Terrane with Baltica during the Ordovician, a rifting between these two regions seems unlikely. Baltica and Scotland were relatively close during the Ordovician, so it is possible that dispersal could have occurred between these two regions directly or through an ancillary region, such as Greenland. However, it is also possible that this pattern is an artifact caused by low diversity, since only one taxon used in this analysis came from the Midland Valley Terrane region.

Finally, my area cladogram (Fig. 2) indicates that deiphonine trilobites originated in some combination of Eastern Laurentia, Bohemia, Armorica, and the Tarim Plate. Tectonic and paleomagnetic evidence suggest that the Tarim plate was part of the Gondwanan landmass during the late Ordovician (Zhou and Zhen 2008). In addition, paleomagnetic data suggests that Bohemia and Armorica were located relatively near one another, and again could have exchanged taxa. Bohemia-Armorica was peripheral to Gondwana during the middle-late Ordovician (Tait et al.1995, Torsvik et al 1996) and dispersal could have occurred between Bohemia-Armorica and Tarim along the northern coasts of the Gondwanan landmass. However, these

regions were separated from Laurentia by the Iapetus ocean. Thus, initial movements by ancestral deiphonine trilobites between Laurentia and Tarim/Bohemia/Armorica probably involved long distance dispersal, perhaps facilitated by the group's putative planktonic larval type (*sensu* Speyer and Chatterton, 1989).

GIS study of trilobites from the cheirurid family Deiphoninae Raymond 1913

Introduction

The end Ordovician represents a unique period in the history of life. It is one of the big 5 mass extinctions, and in terms of the total percentage of species eliminated it may be the second most severe after the Permian-Triassic event. It is associated with a sudden glacial episode that occurred during a time of otherwise marked greenhouse conditions (Berry & Boucot 1973, Sheehan 1973). The cause of this brief icehouse is still a matter of debate, and there are unique patterns of extinction across the event that defy expectation: in particular the extinction patterns of trilobites during the end Ordovician. Trilobites are one of the most diverse and abundant fossil groups known from the Ordovician and were hit particularly hard by the extinction. Further, they have a complex and readily interpretable morphology, and the fossil record preserves both larval and adult forms. Thus, they are particularly well suited for use in a study of patterns and processes of extinction during this interval. One of the distinctive patterns about the extinction vis a vis trilobites is that those whose larval forms have been interpreted by paleontologists as benthic were more likely to survive the extinction than trilobites whose larval forms were interpreted as planktonic (*sensu* Chatterton and Speyer 1989); this is unexpected because organisms with planktonic larvae typically have large species ranges. It has been frequently shown that species with larger geographic ranges typically have lower extinction rates (e.g., Stanley, 1979; Vrba, 1980, Jablonski 1989). Although

these patterns were proposed initially by Chatterton and Speyer (1989) they have not been explored in detail, particularly using modern biogeographic methods, including Geographic Information Systems (GIS). This paper explores the end Ordovician mass extinction by using GIS techniques to estimate species ranges in the diverse Ordovician and Silurian trilobite group Deiphoninae Raymond 1913 in order to ascertain if species with larger ranges preferentially go extinct across the end Ordovician. This subfamily is not only diverse and abundant, but a phylogenetic hypothesis exists for the group (Congreve, Lieberman, and Adrain, to be submitted), which can help provide additional constraints on the stratigraphic ranges of various lineages through the extinction interval. This subfamily was inferred to have a planktonic larval type by Chatterton and Speyer (1989).

Another issue examined herein is whether species ranges gradually reduced in size leading up to the end Ordovician (Ashgill) extinction event. If this were the case it might indicate that there was a subtle, protracted trend towards environmental destruction, perhaps associated with an earlier onset of the end Ordovician glaciation than traditionally accepted. This might in turn suggest that although the mass extinction occurred in the end Ordovician, it had been precipitated, and perhaps had begun much earlier due to the action of environmental forces.

Methods

A database was generated of the occurrence data (in the form of latitude/longitude coordinates) and geologic stages of deiphoninine species using

published literature and museum collections from the Yale Peabody Museum, the Field Museum, and the Museum of Comparative Zoology (Table 3). Latitude and longitude coordinates of fossil localities were typically not provided, so coordinates were calculated using maps and online geographic locator software (such as Google Earth). Since the occurrence data cited in some of the scientific literature was restricted to the city or county level, the latitude and longitude coordinates of the actual localities was not always possible to ascertain, thereby limiting the resolution of my study.

The occurrence data was turned into a database file and then inputted into ArcGIS 9.2 as a point shape file, using the Geographic Coordinate System WGS 1984 projection. Using PaleoGIS (Scotese 2007), these data points were rotated back to their reconstructed positions in the Ordovician-Silurian. PaleoGIS rotates these points by utilizing a tectonic model consisting of two parts: geographic data that defines the plates and a model for capturing the plate movement. The first part (the geographic data) consists of every element that has an independent movement history. These elements are coded with a unique ID and also with the geologic age of their appearance and disappearance. Since it is impossible to change the shape of the plates using ArcGIS, any area that has been reshaped in the past is broken up into a series of independent elements. The second part of the model (the plate movement model itself) integrates information from multiple geologic sources, such as modern plate boundaries, marine magnetic anomalies, hotspot migration, paleomagnetic data, and stratigraphic data including large-scale geologic structures (fault systems, folds, etc.)

and lithofacies with paleoenvironmental and paleolatitudinal importance. This information is used to infer the movement of the plates through time and it is coded in the model by utilizing Euler's spherical principles, which state that the movement of a sphere cap along a spherical shell can be described by the latitude and longitude coordinates of a point and the angle about which that point moves through a great circle path. The actual model is written as a text file that codes the position and movement of every plate (or element) for every time period, and also codes whether movement is relative to the mantle or another plate. Within this file the plates are arranged in a hierarchy, with the plates that have good constraints on movement relative to the mantle (chiefly from hotspot data) having top priority and those plates that are poorly constrained relative to the mantle having lower priority. During a reconstruction, the plates at the top of the hierarchy are positioned first relative to the mantle. The subsequent plates are then added in relative to the top priority plates according to the best evidence available (Rothwell Group, 2007).

For this analysis I used Scotese's plate model to reconstruct my data points. Since any plate model from the Paleozoic lacks direct evidence of plate motion, it is possible that a different model could have yielded a vastly different reconstruction. On the other hand, since my data is mostly constrained to Laurentia (an area that has changed relatively little since the Precambrian), the error imposed by my choice of plate model is most likely minimal.

I generated a total of four map reconstructions; one for each of the geologic stages considered in this analysis (Llandeilo, Caradoc, Ashgill, Wenlock). The

approximate duration of each of these stages was 6 to 9 million years. Therefore, the resolution of my study is somewhat limited because species that I considered to have existed at the same time period might not have been contemporaries. Finer detail would certainly be desirable, but at this time is just not possible because of constraints of the available chronostratigraphic and biostratigraphic data.

Table 3: Database of deiphonine trilobites

Genus	Species	Age	Latitude	Longitude
Sphaerocoryphe	*robusta*	Caradoc	43.271	-75.160
Sphaerocoryphe	*robusta*	Llandeilo-Caradoc	45.423	-75.698
Sphaerocoryphe	*robusta*	Llandeilo-Caradoc	44.306	-78.320
Sphaerocoryphe	*robusta*	Caradoc	61.517	-124.867
Sphaerocoryphe	*robusta*	Caradoc	61.517	-124.850
Sphaerocoryphe	*robusta*	Caradoc	61.483	-124.783
Sphaerocoryphe	*robusta*	Caradoc	61.483	-125.050
Sphaerocoryphe	*maquoketensis*	Caradoc-Ashgill	42.999	-91.657
Sphaerocoryphe	*maquoketensis*	Caradoc-Ashgill	40.751	-92.414
Sphaerocoryphe	*murphyi*	Caradoc	52.257	-7.129
Sphaerocoryphe	*kingi*	Ashgill	54.395	-2.743
Sphaerocoryphe	*dentate*	Ashgill	55.243	-4.855
Sphaerocoryphe	*dentate*	Ashgill	58.298	13.570
Sphaerocoryphe	*dentate*	Ashgill	58.260	13.377
Sphaerocoryphe	*longispina*	Llandeilo	39.002	-78.384
Pseudosphaerocoryphe	*gemina*	Llandeilo	39.002	-78.384
Pseudosphaerocoryphe	*goodnovi*	Llandeilo	44.881	-73.443
Pseudosphaerocoryphe	*goodnovi*	Llandeilo	44.713	-73.459
Pseudosphaerocoryphe	*goodnovi*	Llandeilo	44.608	-73.415
Pseudosphaerocoryphe	*exserta*	Caradoc	-33.244	147.940
Deiphon	*barrandei*	Wenlock	-36.894	149.042
Deiphon	*barrandei*	Wenlock	35.769	-91.624
Deiphon	*barrandei*	Wenlock	52.168	-2.406
Deiphon	*grovesi*	Latest Wenlock	52.509	-2.087
Deiphon	*bainsi*	Latest Wenlock	52.225	-3.101
Deiphon	*ellipticum*	Wenlock	62.417	-127.000

Deiphon	*globifrons*	Wenlock	62.417	-127.000
Deiphon	*globifrons*	Wenlock	57.554	18.590
Deiphon	*globifrons*	Wenlock	57.857	19.050
Deiphon	*globifrons*	Wenlock	57.419	18.152
Deiphon	*globifrons*	Wenlock	57.882	19.164
Deiphon	*globifrons*	Wenlock	57.917	19.067

The reconstructed data points were then projected into the Projected Coordinate System WGS 1984 and used to estimate species ranges. The procedure for these estimations follows Hendricks, Lieberman, and Stigall (2008). Species occurring in only one locality were assigned a range of 3.14 km^2, equivalent to creating a 1 km radius buffer around the locality. For species occurring in two localities, ranges were estimated by calculating the distance between the points, and then the line was assigned a thickness of 2 km to create a rectangle of specifiable area. For species occurring in more than two localities, minimal area estimates were created using polygon shape files, created by connecting the occurrence data points using the shortest distances between them. The area of these polygons was then calculated using the Area Calculator in ArcGIS (Table 4). Higher taxonomic patterns were analyzed, using the phylogeny generated by Congreve, Lieberman, and Adrain (to be submitted) to divide the family Deiphoninae into two monophyletic lineages: the True *Sphaerocoryphe* (containing species belonging to the monophyletic *Sphaerocoryphe*) and the *Deiphon* lineage (containing species belonging to *Deiphon*, and the paraphyletic "*Pseudosphaerocoryphe*"). Range estimations for species within these two lineages were compared to determine if any patterns emerged.

Table 4: Estimated range

Genus	Species	Range (sq km)
Sphaerocoryphe	*robusta* (llandeilo)	536.96
Sphaerocoryphe	*robusta* (caradoc)	505555.81
Sphaerocoryphe	*maquoketensis* (caradoc)	547.04
Sphaerocoryphe	*maquoketensis* (ashgill)	544.98
Sphaerocoryphe	*kingi*	3.14
Sphaerocoryphe	*dentate*	14880.24
Sphaerocoryphe	*longispina*	3.14
Sphaerocoryphe	*murphyi*	3.14
Pseudosphaerocoryphe	*gemina*	3.14
Pseudosphaerocoryphe	*goodnovi*	10.10
Pseudosphaerocoryphe	*exserta*	3.14
Deiphon	*barrandei*	1152.34
Deiphon	*grovesi*	3.14
Deiphon	*bainsi*	3.14
Deiphon	*ellipticum*	3.14
Deiphon	*globifrons*	556.16

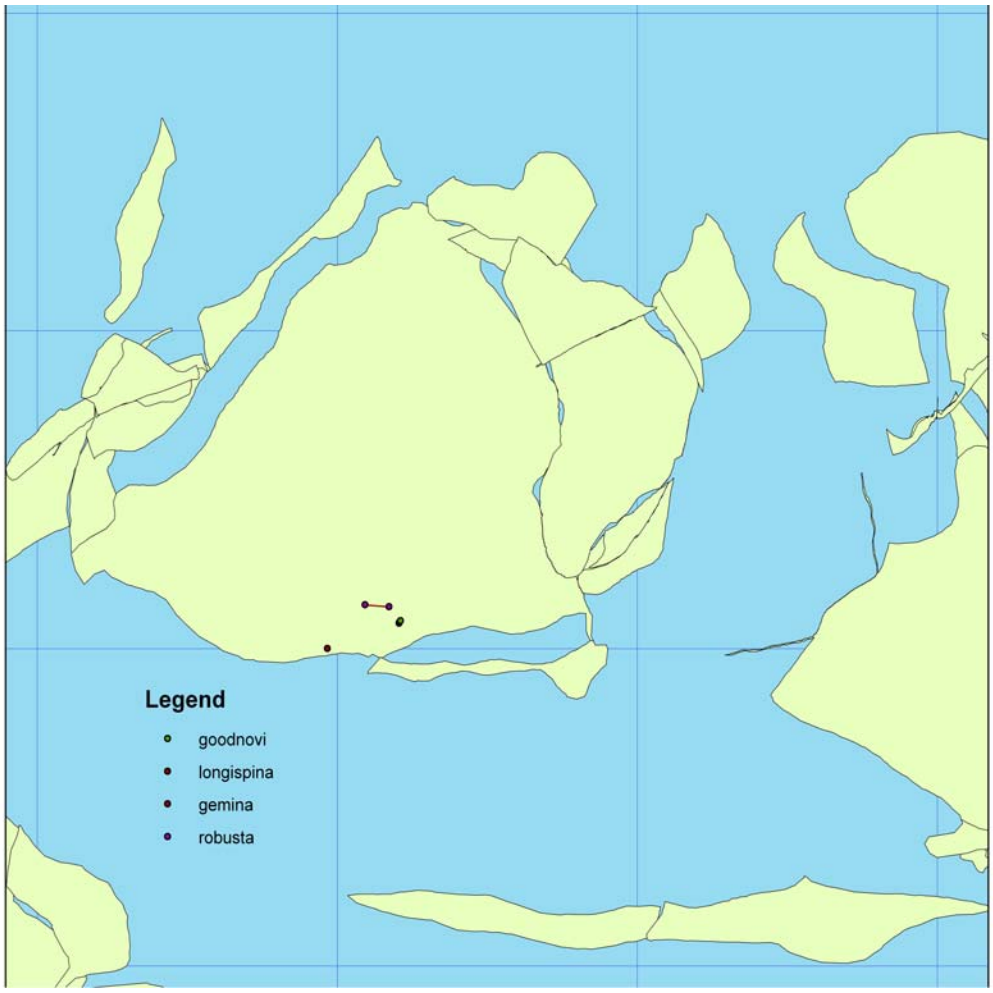

Figure 11: Map of species' ranges during the Llandeilo.

Llandeilo- During this period, species ranges were generally small. Species from both lineages are represented; species belonging to the *Deiphon* lineage (*goodnovi*, *gemina*) appear to have smaller ranges than species belonging to what was referred to as the True *Sphaerocoryphe* lineage.

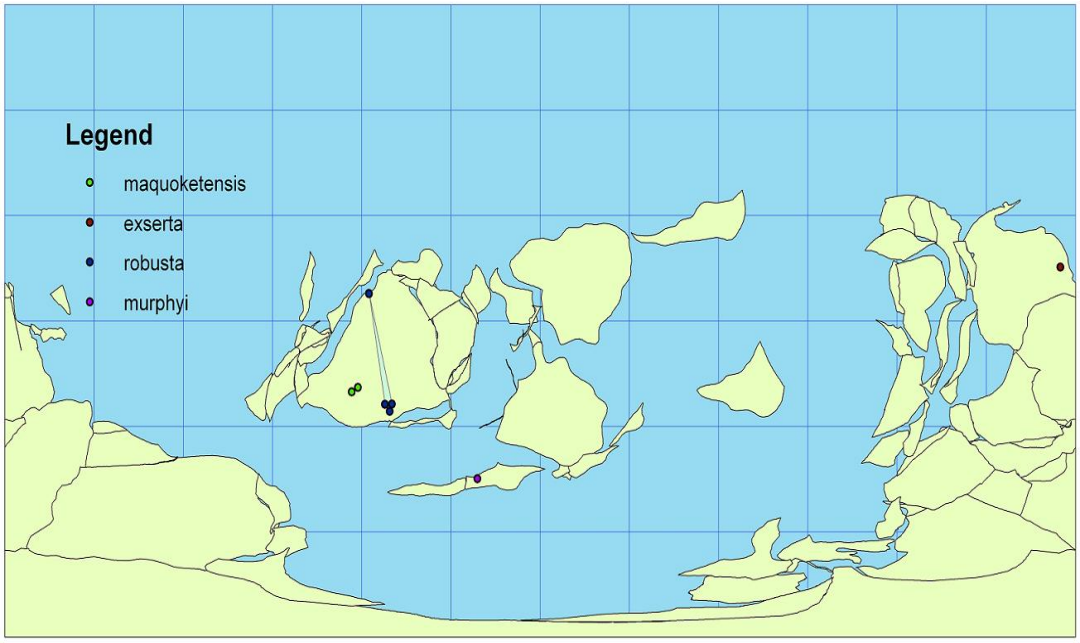

Figure 12: Map of species' ranges during the Caradoc.

Caradoc- During this period, species ranges appear to be larger than those in the Llandeilo: for example, the range of *Sphaerocoryphe robusta* increased substantially in area. Also, only one member of the *Deiphon* lineage (*exserta*) is present during the Caradoc, and it occurs in Australia (a part of the supercontinent Gondwana). This suggests that a major dispersal event from ancestral North America (Laurentia) to Gondwana took place in the Llandeilo or Caradoc.

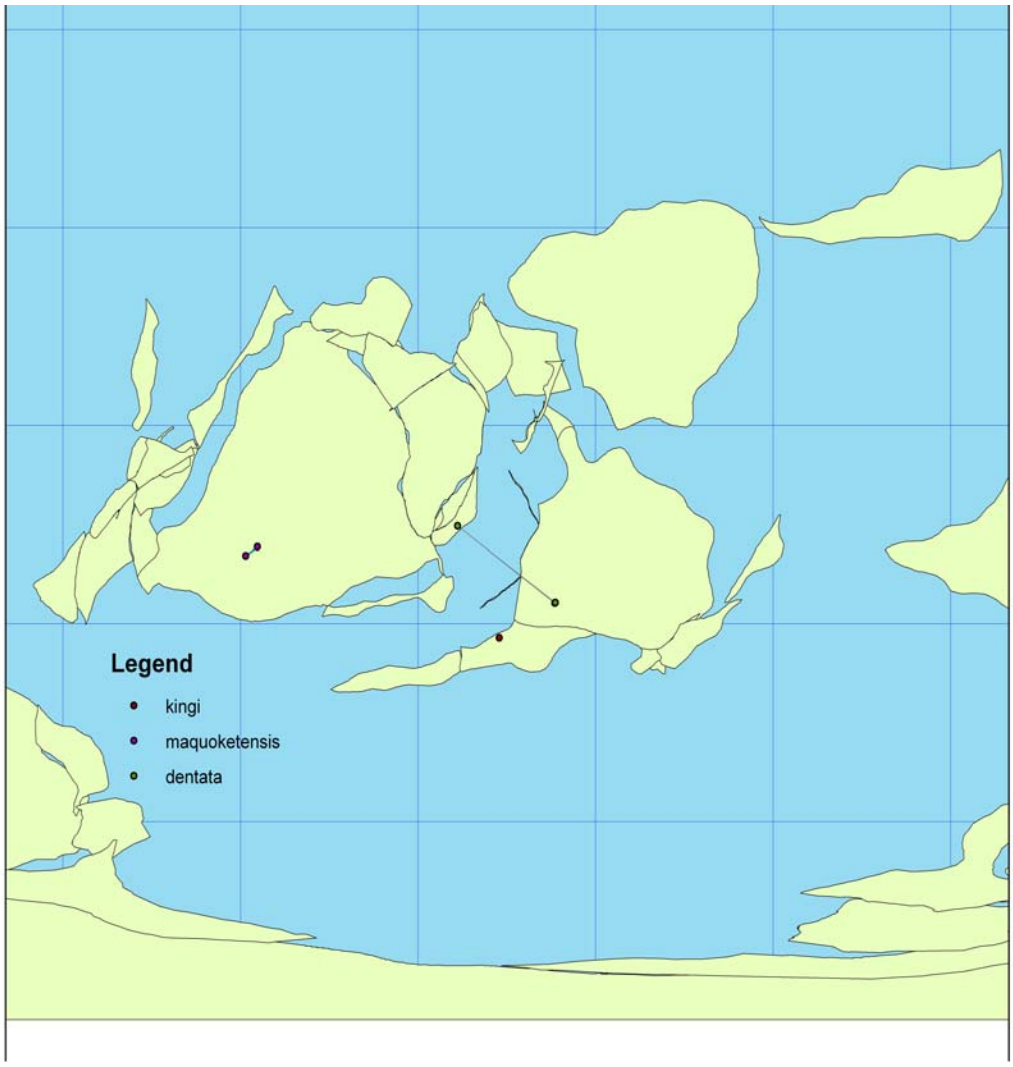

Figure 13: Map of species' ranges during the Ashgill.

Ashgill- Range estimates from this period although smaller than in the Caradoc, are still larger than they were in the Llandeilo. All species from the Ashgill were members of the True *Sphaerocoryphe* lineage. Interestingly, no *Deiphon* lineage trilobites have been recovered from the Ashgill, although this genus survives into the Silurian meaning they must have been extant. Perhaps population sizes of these

trilobites were too reduced for them to be preserved in the fossil record or maybe they were persisting in geographic regions that have not been sampled.

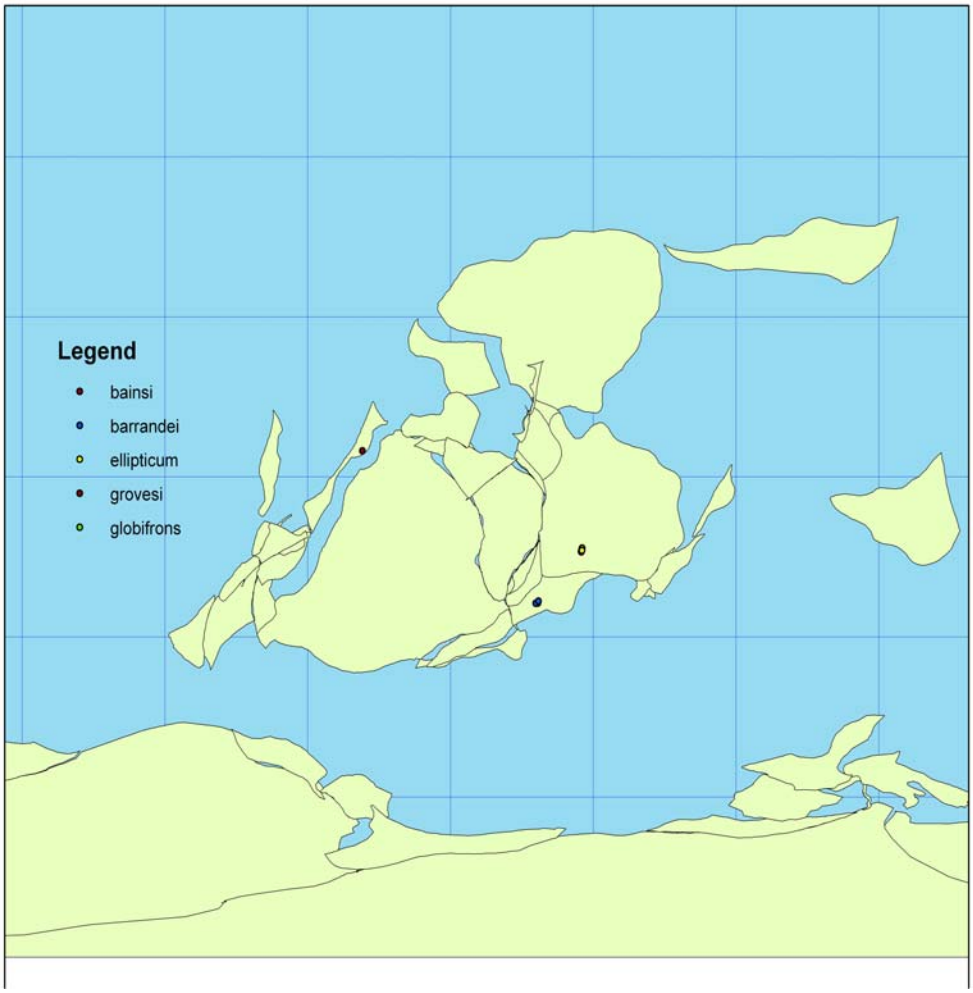

Figure 14: Map of species' ranges during the Wenlock.

Wenlock- All deiphoninine species occurring during the Silurian belong to the *Deiphon* lineage, suggesting that the True *Sphaerocoryphe* lineage went extinct at the end Ordovician event. Species range estimates in the Wenlock are smaller than the

range estimates of the Caradoc, and appear slightly smaller than the estimates from the Ashgill.

Conclusions

Although the data was limited, I conducted a preliminary statistical analysis of my results. First, an ANOVA test was conducted to test if the mean species ranges of the four time periods (Llandeilo, Caradoc, Ashgill, Wenlock) were significantly different from each other. According to the test, the mean species range of the Caradoc differs from the other means with 56.5% confidence (p-value = 0.435). Therefore I fail to reject the null hypothesis that all means are equal (see figure 15 for the confidence intervals generated using ANOVA). If the glacial period at the end Ordovician were a protracted event that started in the Caradoc, I would expect to see significant range contraction from the Caradoc to the Ashgill as species moved towards the equator in response to cooling temperatures, and then subsequent expansion in the Wenlock when the Earth's climate returned to greenhouse conditions. Rather, my data suggests that there is no difference in mean species ranges before, during, or after the extinction, which in turn suggests a rapid onset of glaciation. This pattern is consistent with the Gamma-Ray Burst (GRB) hypothesis (Melott *et al*. 2006) which proposes that the glaciation at the end Ordovician was caused by a nearby GRB that changed atmospheric chemistry and created a sudden onset, yet unstable, icehouse.

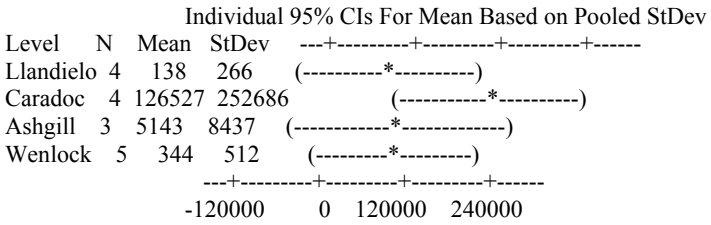

Fig 15: Error bars for the four means were calculated assuming 95% confidence. The stars represent the calculated means for each geologic stage, and the brackets on the left and right of the stars represent the extent of the error. These confidence intervals were generated using Minitab v. 15.1.1.0 (Minitab Inc, 2007).

Two tests were also conducted to see if the mean species range of the *Deiphon* lineage was significantly less than the mean species range of the True *Sphaerocoryphe* lineage: a one-tailed T-test and a one-tailed Mann-Whitney test (a non-parametric equivalent of the T-test). The Mann-Whitney test was used since my data distribution may violate the assumption of normality. For the T-test, the areas were log transformed to satisfy the assumption of equal variances. The p-value for the T-test was 0.109, while the Mann-Whitney test was significant at the level of 0.2374. Using the T-test, I can reject the null hypothesis that the mean range of the *Deiphon* lineage is not less than the mean range of the True *Sphaerocoryphe* lineage with 85% confidence. It does appear that the mean species range of the *Deiphon* lineage is less than the mean range of the True *Sphaerocoryphe* lineage at the .2 level using the non-parametric test, however my data is not significant at the .05 level.

It is possible that these differences in geographic range relate to intrinsic differences in the organisms themselves. For instance, Chatterton and Speyer (1989)

concluded that the entire family containing Deiphoninae had a planktonic larval stage, though not every species within the family could be sampled to make that inference. It is possible that the members of the True *Sphaerocoryphe* lineage had larger ranges because their planktonic larval stage had a longer duration than those of the *Deiphon* lineage, or even that the *Deiphon* lineage may have possessed a benthic larval stage, although this will require additional study beyond the scope of this analysis. Furthermore, in the future I plan to calculate speciation and extinction rates within these two lineages and then compare these rates with the geographic range data in order to see if there is a relationship between inferred larval type and rates of speciation/extinction. This would have profound implications for testing macroevolutionary theories such as species selection.

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